Predator Switching and Optimal Diet: Insights from a Generalized Predator-Prey Model

by

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Abstract

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Improved realism in the description of resource-consumer interaction include the consideration of physiological constraints (e.g., consumer functional response) or behavioural mechanisms, such as resource choice maximising the energy intake or switching behaviour when resources become rare. From the former idea, optimal foraging theory (OFT) has emerged as the premise for optimal diet models (ODM). While OFT and typical ODM are based on the so-called bang-bang (zero-one) rule, i.e., a resource is always taken or ignored upon an encounter, diet models considering switching behaviour are mainly characterized by a disproportionate increase (respectively, decrease) in the number of attacks upon a resource type, when the abundance of the latter increases (respectively, decreases). Though both mechanisms have been proved to promote permanence and stability of resource-consumer dynamics, only ODM considers optimization of predator's food intake. We propose an adaptive optimal diet model (AODM) which considers both the switching behavior (allowing for partial preference) and the global maximization of energy intake, under different levels of consumers' specialization and a generalized Holling type II functional response. In addition, we proved under certain conditions that random foraging is more valuable than adaptive (optimal) foraging.

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Dedications

To my family.

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Chapter 1

Introduction

1.1 Research context and motivation

Mathematical modelling of population dynamics has been for more than three centuries an exciting theme of research for several interdisciplinary researchers, and still continues to be nowadays. Since Malthus' work (1798) on "An Essay on the Principle of Population", several other works regarding population dynamic have been carried out and have led to a proliferation of theories and models that enable investigating the different mechanisms and emergent patterns within populations, communities, meta-populations, etc. Ecology constitutes one of the most concerned areas with mathematical modelling as a contrivance of providing new patterns to get insights into hidden processes. Understanding and describing phenomena within ecological communities using mathematical models remain a challenging work. This is not because ecological systems or communities abound a myriad of species, but because even the interplay of just two species can display complex dynamics to be described ecologically or biologically. This intricacy is caused by the adaptive and evolutionary nature of the different types of interactions within species present in ecological communities. Besides, the mechanisms governing ecological phenomena or processes are fascinating and endued with great importance. Not only do the models developed in that area allow better understanding and the tracking of the ecosystem with all its biodiversity, but these models also enable us to predict and avoid certain natural disasters. In fact, some issues in term of maintaining the balance of the food chain, regarding species invasion and extinction control,

and climate change (which constitutes one of the current major worldwide concern) have been tackled using mathematical models developed for ecological systems. Moreover, these models constitute valuable tools in some other fields of research, such as economics, insurance, social sciences.
The present work is based on one of the well known and intriguing relationships observed in any natural environment; the battle for survival, also denoted by predation. Predation is the fact whereby an organism dubbed predator or consumer kills another (prey or resource) for nutritional purposes [5]. This phenomenon has been for a long time and still continues to be a central theme of study for ecologists as well as for mathematicians passionate about ecology. This is in part due to its universal existence and the impressive mechanism underlying it. To gain an insight into the dynamic of the relationship between predators and their prey, several researchers resorted to mathematics and their efforts resulted into mathematical models for predator-prey interactions among which the pioneer work of Lotka and Volterra in the mid 1920s.
Since Lotka-Volterra's work, there has been a growing interest to understand and mathematically represent foraging strategies. In that sense, Michael Rosenzweig and Robert MacArthur suggested a model that accounts for limited resources. Most important was the work of Holling [17] on functional responses which constitute the core component of their predator-prey system. Besides, much attention has been paid to multi-species systems-systems which consist of at least three interacting species (two prey populations and one predator population, for instance)- which tend to be the case of natural environments.
Improved realism in the description of predator-prey interactions includes the consideration of physiological constraints (e.g., predator functional response) or behavioural mechanisms, such as resource choice maximising the energy intake or switching behaviour when resources become rare. From the former idea, optimal foraging theory (OFT) has emerged as the premise for optimal diet models (ODM). While OFT and typical ODM are based on the so-called bang-bang (zero-one) rule, i.e., a resource is always taken or totally ignored upon an encounter, diet models considering switching behaviour are mainly characterized by a disproportionate increase (respectively, decrease) in the number of attacks upon a resource type, when the abundance of the latter increases (respectively, decreases). Though both

mechanisms have been proven to promote permanence and stability of resource-consumer dynamics, ODM only considers optimization of predator's food intake. We believe that for a better understanding and description of a multi-species food chain, a mechanistic predator-prey model should incorporate simultaneously certain behavioural mechanisms such as predator switching towards the most abundant prey type and the maximization of food intake.
Thus, in the present work, we aim to propose an adaptive optimal diet model (AODM) which considers both predators switching behaviour (thus allowing for partial preference) and maximization of food intake, under different levels of consumers' specialization or adaptiveness and a generalized Holling's type II functional response that includes allometry scaling in its parameterization. In addition, analytical and numerical investigation of the influence of some key parameters on the AODM on its dynamic will constitute the secondary objectives.

1.2 Fundamentals and outline of the project

This part gives the minimum necessary requirements, mathematical background in differential equations required to understand or to follow at ease the remaining part of this document. The concepts of functions, derivatives and ordinary differential equations constitute the main idea of this section. Also, the thesis outline will be described briefly.

1.2.1 Functions, Limits and Continuity

From a mathematical point of view, a *function* can be viewed as a rule or relation between two sets. The first set consists of the different inputs and it is referred as the function's domain; whereas the second set, usually called the function codomain, contains the possible outputs (range) and possibly some other elements. In addition, functions have the property that any element of its domain yields exactly to one of the different outputs. Functions are described by equations. $f(x) = x^2$ (or simply $f = x^2$) is an example of function; having name 'f' and described by the relation that for each element 'x' taken as input, the function 'f' returns the square (x^2) of the given element as output and x in that case is called the independent variable. Its

domain is therefore all possible x values that can be plugged into the equation representing f and the range in that case consists of all the values $f(x)$. Thus, a function denotes the dependence of one quantity on another. Besides, a function can be univariate or multivariate. A univariate function represents function that depends on one argument i.e., which takes as input exactly one object or element while a multivariate function depends on more than one argument. Generally, given some sets A_1, A_2, ..., A_i, ..., A_n, A and B, one can define a multivariate function as;

$$\begin{aligned} f: \quad & A_1 \times A_2 \times ... \times A_i \times ... \times A_n \to B \\ & (x_1, ..., x_i, ..., x_n) \mapsto f(x_1, ..., x_i, ..., x_n), \end{aligned} \tag{1.1}$$

and a univariate function as;

$$\begin{aligned} f: \quad & A \to B \\ & x \mapsto f(x). \end{aligned} \tag{1.2}$$

After having defined a function, one of the fundamental concepts which follows is that of *limit*. The limit of a function describes the behaviour of that function near a particular given input. Given a function $f(x)$ and a point x_0, the limit of $f(x)$ at x approaching x_0 is noted as;

$$\lim_{x \to x_0} f(x).$$

Mathematically, the concept of limit is formalized by the following general definition.

Definition 1.2.1. *Let $f : \mathbf{D} \subseteq \mathbf{R}^n \to \mathbf{R}$ be a function defined for all $x = (x_1, x_2, ..., x_n)$ in some open region $\mathbf{D} \subseteq \mathbf{R}^n$ and $x_0 = (x_{0_1}, x_{0_2}, ..., x_{0_n})$ a fixed point which may or may not be in $\mathbf{D}$. A point $L \in \mathbf{R}$ is said to be the limit of $f(x)$ as $x \in \mathbf{D}$ approaches x_0 if and only if for every $\epsilon > 0$, there exists a $\delta > 0$ (which usually depends on ϵ) such that for every $x \in \mathbf{D}$, the expression $0 < \| x - x_0 \|_n < \delta$ implies $| f(x) - m | < \epsilon$.*

For example, the function $f(x) = 7x - 5$ has 9 as limit when x approaches 2. To show that using the definition 1.2.1, we can work backward as follow to find the δ:

$$\begin{aligned} | 7x - 5 - 9 | < \epsilon \quad & \Rightarrow | 7x - 14 | < \epsilon \\ & \Rightarrow | x - 2 | < \frac{\epsilon}{7}. \end{aligned}$$

Thus, for any chosen $\epsilon > 0$ one could take $\delta = \frac{\epsilon}{7}$. The concept of limit has some properties such that the limit of sum, product, quotient of functions is equal respectively, to the sum, product and quotient of their limits. Another fundamental aspect that can be discussed once a function has been defined is that of *continuity*.

Definition 1.2.2. *Let* $f : \mathbf{D} \subseteq \mathbf{R}^n \rightarrow \mathbf{R}$ *be a function defined for all* $x = (x_1, x_2, ..., x_n)$ *in some open region* $\mathbf{D} \subseteq \mathbf{R}^n$ *and* $x_0 = (x_{0_1}, x_{0_2}, ..., x_{0_n}) \in \mathbf{D}$ *a fixed point. The function* f *is said to be continuous at* x_0 *if and only if for every* $\epsilon > 0$, *there exists a* $\delta > 0$ *(which usually depends on* ϵ*) such that* $\mid f(x) - f(x_0) \mid < \epsilon$ *for every* $x \in \mathbf{D}$ *and* $0 < \parallel x - x_0 \parallel_n < \delta$. *This definition 1.2.2 simply means that* $f(x_0)$ *and* $\lim_{x \rightarrow x_0} f(x)$ *exist and that this limit is equal to* $f(x_0)$*; i.e.,* $\lim_{x \rightarrow x_0} f(x) = f(x_0)$.

1.2.2 Differentiation, Differential Equations and Initial Value Problems

Having defined a function, one could also gauge the sensibility to the change of the function output with regard to the change of its input. This describes the notion of *derivative* which constitutes an essential tool of calculus. Mathematically, a derivative of a given function $f(x)$ with respect to x is given as the function

$$f'(x) = \lim_{h \rightarrow 0} \frac{f(x+h) - f(x)}{h}. \tag{1.3}$$

The function $f'(x)$ that represents the derivative is usually read as f *prime of* x and can also be noted as $\frac{d}{dx} f(x)$. When the limit in the definition 1.3 does not exist, the derivative of the function $f(x)$ does not exist either. Note if the function f is a function of two or more independent variables, i.e we have $f(x_1, x_2, ..., x_n)$, then the derivative of f with respect to one of the variable x_i is called *partial derivative* of f with respect to x_i and generally symbolised as $\frac{\partial}{\partial x_i} f(x_1, x_2, ..., x_n)$ or simply $\frac{\partial f}{\partial x_i}$. The partial derivative of a function f with respect to one of its variable x_i is defined as

$$\frac{\partial f}{\partial x_i} = \lim_{h \rightarrow 0} \frac{f(x_1, x_2, ..., x_{i-1}, x_i + h, x_{i+1}, ..., x_n) - f(x_1, x_2, ..., x_{i-1}, x_i, x_{i+1} ..., x_n)}{h}.$$

The process by which we get the derivative of a function is called *differentiation* and for a given point x_0, if $f'(x_0)$ exists, then the function f is said to be

differentiable at x_0. From this concept of differentiability and the concept of continuity, came up the following theorem.

Theorem 1.2.3. *If a function $f(x)$ is differentiable at x_0 then $f(x)$ is continuous at x_0 (this theorem also holds for functions of several variables).*

Proof. Let $f(x)$ be a function and x_0 be a point. Assume that $f(x)$ is differentiable at x_0. Thus, we have

$$\begin{aligned} f'(x_0) &= \lim_{h\to 0} \frac{f(x_0+h)-f(x_0)}{h} \\ &= \lim_{x\to x_0} \frac{f(x)-f(x_0)}{x-x_0}, \text{ by setting } h = x - x_0. \end{aligned} \tag{1.4}$$

Besides, we have

$$f(x) - f(x_0) = (x-x_0)\frac{f(x)-f(x_0)}{x-x_0}, x \neq x_0$$

Setting limit both sides of this expression yields to

$$\begin{aligned} \lim_{x\to x_0}(f(x)-f(x_0)) &= \lim_{x\to x_0}(x-x_0)\frac{f(x)-f(x_0)}{x-x_0} \\ &= \lim_{x\to x_0}(x-x_0) \times \lim_{x\to x_0}\frac{f(x)-f(x_0)}{x-x_0} \\ &= 0 \times f'(x_0) \qquad (1.5) \\ &= 0 \qquad (1.6) \end{aligned}$$

Thus, we get $\lim_{x\to x_0} f(x) = \lim_{x\to x_0} f(x_0) = f(x_0)$, which prove that $f(x)$ is continuous at x_0. The proof when f is a multivariate function is omitted deliberately because in this project we will be dealing much with derivatives than partial derivatives.

A *differential equation* is an equation that contains derivatives. The derivatives can be either ordinary; in which case the equation is called an ordinary differential equation; or partial and in which case the equation is a partial differential equation. Besides, differential equations have a wide application, mostly concerned with modelling phenomenon in engineering, biological sciences, social sciences, economic to cite a few examples. Mathematically, the study of differential equations mainly implies finding solutions; i.e., functions that satisfy the given equation. Separation of variables, the integrating factor and substitution are some of the techniques

used to solve analytically first order differential equations. However, not all differential equations can be processed analytically; in which cases the so-called numerical methods (Euler's method, Midpoint method, Runge-Kutta method, etc.,...) that give approximate solutions to the differential equations are used. In this project, we will be dealing with systems of first order differential equations that cannot be solved analytically.

1.2.3 Thesis Outline

We first give a general review of the fundamental mathematical models for predator-prey systems (Chapter 2). The paradigm of functional responses will be discussed in detail and the concepts of predator switching and optimal foraging and their effects on predator-prey systems will constitute an important point of this chapter.
In chapter 3, based on the generalised Holling's disk equation and considering allometry scaling theory, we propose a generalized mechanistic resource-consumer model that combines maximal feeding and predator switching. Then, we provide in Chapter 4 an analytical analysis for such formulation and numerical results of our proposed model according to different aspects. Besides, a discussion on the different results will also be provided. In Chapter 5, we draw the conclusions of our work, highlighting the main elements we introduced and proposing further works for the present project.

Chapter 2

State of The Art: The Mathematics of Hunting

In this chapter, we review the fundamental mathematical models that have been playing a key role with regard to the theory of predation. The paradigm of functional responses-one of the most important factors on which relies the development of predator-prey interaction models-will be discussed. Besides, the concepts of adaptive and optimal foraging which constitute the baseline of this project will be introduced.
Also, the term predator and consumer; prey and resources will be used interchangeably, although they may have biologically different meanings. That is, consumer and resource will be used in the broadest sense, so that they refer to predator and prey respectively.

2.1 Predator-prey Theory and Formulation of Functional Responses

Though predation is a phenomenon as ancient as life and which has played important roles in some of its passages, the set of principles behind predation took shape from 1838 onwards. Indeed, Predator-prey theory has evolved from the Malthusian population theory through the Lotka-Volterra system, Rosenweig-MacArthur system and the paradigm of Holling's functional responses which constitute the core component for any formulation of resource-consumer model.

2.1.1 From the Malthusian Theory to Predator-Prey Theory

1. Malthus' Equation

   The pioneer theoretical treatment of population dynamics originated from the late 1790's with Thomas Robert Malthus' work; *An essay on the principle of population*; in which it had been argued that populations grow logarithmically while the resources on which they depend increase arithmetically or remain constant [6]. Four decades had been necessary to formulate the Malthus' principle into a mathematical expression.

   In fact, the well know logistic equation for population growth;

   $$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right),$$

   where V represents the population density and K the carrying capacity of the environment (the maximum population size that can be supported by the environment) represents the mathematical model of the Malthusian principle derived in 1838 by Pierre-François Verhulst. Though this expression successfully described the dynamics in laboratory as well as in the field of some single-species populations, it received certain criticisms largely due to the simplicity associated with it [6]. Besides, when it comes to describing interactions between species, the logistic equation appears to be inappropriate and further research on population dynamics had led to the primary mathematical system describing the dynamic of populations at different trophic levels; the Lotka-Volterra model.

2. Lotka-Volterra System

   The first mathematical model incorporating interacting species is the Lotka-Volterra system which was independently derived by Alfred Lotka and Vito Volterra in 1926. The system consists of two non-linear differential equations where one of these equations describes the resource population dynamics and the other the consumer population dynamics. The model was formulated according to some assumptions on the prey and predator population growth. Assumptions made in modelling the prey population consist of:

i. predation is the only limiting factor of the prey population growth. That is, the prey population is supposed to have an unlimited supply of food and space. This implies an exponential increase of the prey population density in the absence of consumers; which can be mathematically described by a linear rate of change,

$$\frac{dV}{dt} = rV.$$

r here is denoting the intrinsic or per capita rate of increase of the prey population and it is also called the Malthusian parameter after Thomas Robert Malthus [14]. This exponential growth does not account for movement in and outside the population, i.e., there is no immigration and emigration and thereby the population of species is considered closed and therefore r can be defined as the difference between the per-capita birth rate b and the per-capita death rate d for the prey population. Thus, b and d are measured per individual per unit time and therefore have respectively unit of [births/(individual·time)] and

[deaths/(individual·time)]. The definition of b, d, implies that the measurement unit of r is individuals per individual per unit time [individuals/(individual·time)] [14]. Besides, r might be positive if $d < b$ and in that case the prey population increases exponentially ; negative if $d > b$ and thus the prey population goes extinct; or null if $b = d$ and in which case the prey population remains constant over time. In the Lotka-Volterra model, since prey has unlimited food resources and space, r is considered to be positive.

ii. prey population suffers losses only in the presence of predators and they encounter each other randomly (law of mass action) and the environment is supposed to be homogeneous, i.e the prey do not have spatial or temporal refuges. Those losses are considered proportional to the prey population density and therefore represented by a linear function of V [14]

$$\frac{dV}{dt} = rV - aVP, \tag{2.1}$$

with P denoting the predator population density and the term aV representing the number of preys taken by an individual preda-

tor per unit time foraging. It also defines what is called "functional response". Detailed discussions about this function constitute the purpose of the next section.

Assumptions made in modelling the predator population growth in the Lotka-Volterra model are twofold. First, it is assumed that the prey is the only food resource within the scope of the predator. That is, there is no other alternative food sources for the predator besides the specific prey V. Thus, in the absence of prey V, the predator will die out with a per capita death rate $m > 0$ (which can be seen as the instantaneous death rate d seen earlier), i.e., the predator population decreases exponentially:

$$\frac{dP}{dt} = -mP.$$

The second assumption is that the predator population experiences a positive growth only in the presence of prey and this growth is increased when the prey population increases and it is proportional to the number of prey taken aV;

$$\frac{dP}{dt} = caVP - mP, \tag{2.2}$$

where c denotes the conversion growth efficiency and represents the predator's ability to convert each eaten prey into predator's birth. Note that c is a positive parameter in between zero and one ($0 < c < 1$) since an individual cannot grow more than the biomass of resource ingested.

From the different assumptions made on both prey and predator population growth, the Lotka-Volterra system is formed as a combination of the equations (2.1) and (2.2):

$$\begin{cases} \dfrac{dV}{dt} = rV - aVP \\ \dfrac{dP}{dt} = caVP - mP. \end{cases}$$

Though the Lokta Volterra system has been widely used, most of the assumptions made in deriving that model seem unrealistic in the real world. Indeed, the resources cannot grow indefinitely and therefore

the prey population in the Lokta Volterra system might not grow indefinitely, but will ultimately reach a maximum prey abundance that can be supported by the environment. Besides, predators can not always increase their consumption when prey population increases; predators may be satiated or limited by the time required to catch and consume each prey item [14]. Those observed limitations have led to the emergence of more realistic models among which the Rosenzweig-MacArthur model.

3. Rosenzweig-MacArthur Model

   The Rosenzweig-MacArthur model of prey-predator interaction can be seen as an extension of the Lotka-Volterra system in the sense that most of the assumptions made on formulating that model are those of the Lotka-Volterra system. Except, the fact that the exponential growth for the prey population supposed in the Lotka-Volterra model was substituted by a logistic growth function (to allow restriction of the prey population growth by the capacity of the environment, even in the absence of consumers) and the limitation of prey consumption by the necessary time needed by a predator to catch and process a prey item (handling time h), there are no other considerable changes [12]. Thus, the dynamic of the prey population in the Rosenzweig-MacArthur model is given by:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \frac{aV}{1 + ahV}P. \tag{2.3}$$

   The term $\frac{aV}{1+ahV}$ corresponds to the functional response (refer to the next section for further details). The carrying capacity K has the unit of number of individuals.

   There are no substantial changes in modelling predator population. However, since the function representing losses has changed, the growth function of the predator population will vary accordingly. Hence, the change in predator population over time is defined as:

$$\frac{dP}{dt} = \frac{caV}{1 + ahV}P - mP; \tag{2.4}$$

   c and m denoting the same parameters as in the Lotka-Volterra system.

The Rosenzweig-MacArthur model is therefore defined by the system set up by the equations (2.3) and (2.4);

$$\begin{cases} \dfrac{dV}{dt} = rV\left(1 - \dfrac{V}{K}\right) - \dfrac{aV}{1+ahV}P \\ \\ \dfrac{dP}{dt} = \dfrac{caV}{1+ahV}P - mP. \end{cases}$$

The Lotka-Volterra and Rosenzweig-MacArthur systems constitute the simplest predation models which attempted to describe and predict the dynamics of predator-prey interactions. Further suggested models in the literature rely basically on these two models. In general, some other factors that occur in natural systems have been incorporated for better ecological plausibilities and understanding. The presence of refuge places for prey, the presence of alternative food resources for the predator, age structure, Allee effect, different functional response forms are for instance some the additional components considered.

2.1.2 Formulation of Functional Responses

Though the idea behind the term "functional response" was set out in the years 20s in Lotka and Volterra's works, this term was first used and explicitly described by Solomon [31]. Defined as the way in which the number of prey eaten per predator over a short period changes with prey density [26], functional response constitutes the key element that affects the dynamic of predator-prey systems. Some of the main features explicitly covered by the concept of functional response, according to the description given by [31] include:

i. Functional response defines the changes in the density of prey/resources consumed as a function of resource density.

ii. It represents the per capita rate, i.e. the feeding rate by an individual predator.

iii. Functional response can possibly be unbounded although it probably has some bounds.

Thus, briefly put, the term functional response can be then referred to the change in the population density of resources consumed by an individual predator per unit of time as resources density changes.
Since the pioneer work of Holling [17, 18], a new trend in mathematical ecology for describing predation systems has been to derive more sophisticated functional response models that account for more realistic biological sense in their parameterizations. The different functional response forms suggested in the literature have evolved from single-species resource-dependant functional responses through predator-dependant, multi-species resource and with the incursion of preference, switching and diet choice.

1. Prey-Dependant Functional Response Models

   The traditional prey-dependant functional responses consist basically of the Holling's forms and the threshold functional response, which were primarily developed for single-species (one type of species as resource and one as a consumer) interactions. The Holling's functional response forms were derived on the basis of experiments to investigate how the predator's feeding rate is related to the resource density. From those experiments, Holling described four general forms of functional responses dubbed Type 1, Type 2, Type 3 and Type 4 [13, 22].

   Though all those functional responses were initially defined for single-species systems, the next logical step had been to derive the corresponding models for multi-species systems (system considering several types of species as resources and one or several consumer types), thus adding more ecological realism. In this section, we will not consider explaining explicitly how the models for multi-species systems have been derived. Instead, for each form of single-species functional response we will be discussing, its associated expression for multi-species systems will be stated.

   i) Type 1 functional response

      The assessment of the formulation of the Type 1 functional response is usually disregarded in the literature, but following [14], the Type 1 formulation is based on the assumption that some

predators (species such as filter feeders) do not need handling time for their prey. Thus, it is described by a linear relationship between the predator's capture coefficient and the prey population density. Therefore, the Type 1 response is given by:

$$F(V) = aV, \tag{2.5}$$

which represents the non-satiating expression of the Type 1 response. However, Type 1 response can be rectilinear such that it attains a maximum 'b' for resource densities beyond a certain threshold 'n'. Therefore, Type 1 is generally described as follows [13]:

$$F(V) = \begin{cases} aV = \frac{b}{n}V, & \text{for} \quad V \leq n, \\ b, & \text{for} \quad V > n. \end{cases}$$

Due to the fact that Type 1 functional response does not account handling time for resources in its formulation, the predator's response model for multi-species systems remains similar as for single-species system. Though the different types of species involved in such system (multi-species systems) may differ in their capture coefficient.

ii) Type 2 functional response

The Type 2 response, also referred as Holling's disk equation, constitutes the most used form for describing predator functional response to prey density and has been considered as the base in most of the afterwards formulations of functional responses. Type 2 formulation supposes explicitly that a consumer spends all its time foraging and that time is mainly assigned to two activities; *searching for* and *handling of* resources. If we denote by T the total time that the forager disposes, T_s and T_h the time spent respectively on searching for and handling of resources, the Type 2 response can be derived accordingly considering the following equalities;

$$T = T_s + T_h, \tag{2.6}$$

$$V_c = aT_sV, \tag{2.7}$$

$$T_h = hV_c, \tag{2.8}$$

with V_c denoting the number of prey captured. From the equations 2.6 and 2.8, we can rewrite equation 2.7 as $V_c = aV(T - hV_c)$ which, simplifies to

$$V_c = \frac{aVT}{1 + ahV}.$$

And the Type 2 response; also known as the Holling's disk equation is therefore given as:

$$F(V) = \frac{aV}{1 + ahV} \tag{2.9}$$

Graphically, the representation of Type 2 2.9 with respect to the resources densities defines a concave downward curve (see Figure 2.1). Thus, Type 2 exhibits a decelerating intake rate with increasing resource abundance. This behaviour tends to allow safety for prey at high densities and it increases the risk of being eaten at low densities of resource and therefore leads to a destabilised system [36].

The corresponding Type 2 response form of a multi-species system is defined by considering the handling time needed and the capture coefficient for the different types of resource present in the system. Thus the handling time of a species of each type is defined by taking into account the handling time for all the different species in the system. Generally, Type 2 functional response form of a species of type i in a multi-species system is defined [1] as:

$$F(V_i) = \frac{a_i V_i}{1 + \sum_j a_j h_j V_j}.$$

iii) Type 3 functional response

Sometimes referred to the functional response for vertebrate, the mathematical formulation of the Type 3 response is not straightforward as the Type 2 response. For a single-species system, it is usually given by;

$$F(V) = \frac{\widehat{a}V}{1 + \widehat{a}hV}, \quad \text{where} \quad \widehat{a} = aV^n \quad (\text{with} \quad n > 0). \tag{2.10}$$

Conventionally, 'n' is assumed equal to 1 [13, 22, 12].

Conversely to the attack rate for Type 2 which is linear, we note that the Type 3 rate of capture consists of the square of the resource population density V. This leads to an S-shaped or sigmoidal curve [17, 13, 12, 36] having the same behaviour as Type 2 at high resource densities. Moreover, the Type 3 response has an accelerating behaviour at low resource densities (see Figure 2.1) which tends to stabilize the interactions between a predator and its prey. Generally, the Type 3 response is expressed as;

$$F(V) = \frac{aV^m}{1 + ahV^m}, \quad m > 1$$

and often dubbed as the "generalized form" since Type 1, Type 2 and the aforementioned Type 3 (with $n = 1$) can be derived from that expression. Indeed, Type 1 is obtained when $h = 0$ and $m = 1$; and when $h \neq 0, \quad m = 1$ and $h \neq 0, \quad m = 2$, we get back respectively to the Type 2 and the Type 3 (with $n = 1$) forms.

Taking the capture coefficient $\widehat{a}$ as a power function of prey densities is not the unique way to derive an S-shaped response. Some other forms to describe the Type 3 functional response have been proposed. Indeed, Type 3 response can be also obtained when $\widehat{a}$ is modelled as an increasing function with resource densities that continuously decelerates till reaching an asymptotic maximum. Thus, the per capita feeding rate takes the same form as the expression 2.10 but with $\widehat{a} = \frac{aV}{1+bV}$, and $\frac{a}{b}$ representing the maximum asymptotic value of $\widehat{a}$ [22], that is

$$F(V) = \frac{aV^2}{1 + bV + ahV^2}.$$

Another way to define Type 3 response it obtained by assuming that $\widehat{a}$ is a linear function of resource density, i.e. $\widehat{a} = a + bV$; thus, reducing the equation 2.10 to

$$F(V) = \frac{aV + bV^2}{1 + ahV + bhV^2}.$$

Multi-species model for Type 3 had been proposed and it is gen-

erally defined for each prey species of type i by:

$$F(V_i) = \frac{a_i V_i^{n+1}}{1 + \sum_j a_j h_j V_j^{n+1}}, \quad n \geq 1.$$

iv) Type 4 functional response

Unlike the aforementioned Holling's forms (Type 1, Type 2 and Type 3) which follow a monotonous increase with prey density (i.e., increase till reaching a maximum at some resource density, then become constant at higher density), the Type 4 response does not imitate this pattern. Type 4 functional response is defined by using equation 2.10 and setting the capture coefficient $\widehat{a} = \frac{1}{a+bV^2}$. Thus we have a decreasing behaviour with resource density, i.e., $\widehat{a} \to 0$ when $V \to \infty$. Though, there is a maximum that this Type 4 response reaches at an intermediate resource density, it decreases at higher resource density (refer Figure 2.1), which is justified by resource toxicity (in microbial systems) and/or predator confusion [13, 22]. Type 4 for single-species interactions is expressed as:

$$F(V) = \frac{V}{a + hV + bV^2}, \tag{2.11}$$

which generalises to

$$F(V_i) = \frac{V_i}{(a_i + b_i V_i^2)\left(1 + \sum_j \frac{h_j V_j}{a_j + b_j V_j^2}\right)}$$

for a multi-species system.

v) Threshold functional response

This form of functional response is associated with the general assumption that there is a resource density threshold below which no intake takes place. That is, a predator is unable to feed below this threshold. This functional response bears Type 2 behaviour (refer Figure 2.1) above its threshold and it is viewed as an extreme case of Type 3 response with an initial accelerating phase equals to zero [13]. The Threshold response form is obtained by

considering the Expression 2.10 and defining $\widehat{a}$ as:

$$\widehat{a} = \begin{cases} a\left(1 - \dfrac{V_t}{V}\right) & \text{if} \quad V > V_t; \quad V_t\text{: threshold value,} \\ 0 & \text{otherwise,} \end{cases}$$

which results in:

$$F(V) = \begin{cases} \dfrac{a(V - V_t)}{1 + ah(V - V_t)} & \text{if} \quad V > V_t, \\ 0 & \text{otherwise} \end{cases} \tag{2.12}$$

for single-species interactions. The threshold response is best suited to describe predator-prey dynamics in the presence of prey refuge. Thus, at low densities, prey are invisible or non-catchable because they can remain hidden in their refuge and can only be within the predator's scope once the refuge is full and therefore intake might occur.

Regarding the multi-species' case, the Threshold functional response is associated for each species of type i with the capture coefficient $\widehat{a_i}$ defined as follows ([22]):

$$\widehat{a_i} = \begin{cases} a_i\left(1 - \dfrac{V_{i_t}}{V_i}\right) & \text{if} \quad V_i > V_{i_t}; \quad V_{i_t}\text{: threshold density of } V_i, \\ 0 & \text{otherwise.} \end{cases}$$

Thus, the functional response in that case is expressed as

$$F(V_i) = \frac{a_i(V - V_{i_t})}{1 + \sum_j a_j h j (V_j - V_{j_t})}, \quad \text{with } a_i(V - V_{i_t}) = 0 \text{ if } \quad V_i < V_{i_t}.$$

These different forms of response we described are not the only resource-dependant functional responses that have been developed in the literature. In fact, others models describing resource-dependant responses exist, though they roughly have the same graphical representation form as Type 2, Type 3 or Type 4. For further review of functional responses, the works of [13] and [4] should be considered.

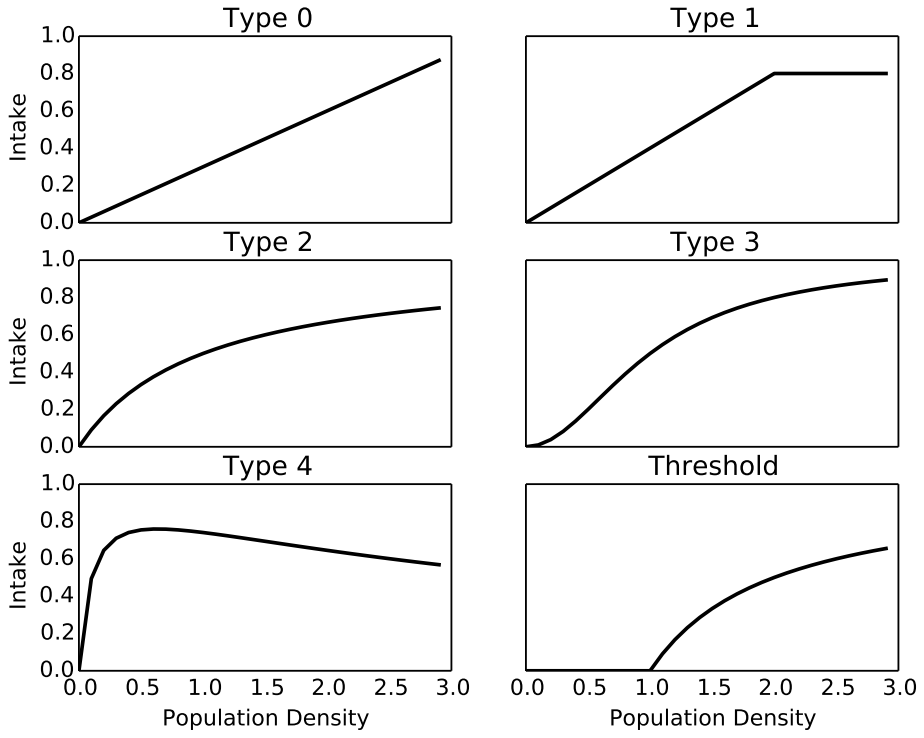


Figure 2.1: Functional Responses Forms

2. Predator Density-Dependent Functional Responses.

   Generally, the dependence of a functional response to the predator density is assumed to be of negative effect, and referred as "interference" or positive effect, and referred as "facilitation" [22]. Incorporating predator facilitation or interference into a functional response presupposes the predator attack rate is a function dependant on the predator density. A general expression of functional response that accounts for predator interference or facilitation and from which arise most of the models of predator density-dependant functional responses has been discussed in the literature. For any species of type i, Koen-Alonso [22] defined a general expression to denote the predator's attack/capture rate as:

   $$C_i = p_i g_i m_i, \tag{2.13}$$

   where C_i is the predator attack rate with respect to the resource of type i and p_i, g_i, m_i are respectively a selection factor, a prey density-dependant factor and predator density-dependant factor.

The selection factor p_i is defined either as a constant or a function of some or all of the different types of species involved in the system, that is;

$$p_i = \begin{cases} c, & \text{where c is a constant,} \\ & \text{or} \\ f(V_1, ..., V_i, ..., V_n), & \text{where n represents the total types of species,} \\ & \text{or} \\ f(V_j, .., V_k), & \text{where } j, k \in [1,\ n]. \end{cases}$$

This factor simply represents the effect of alternative food resources choice on the attack rate C_i and it is viewed as the probability of preying on a specific prey type and therefore $0 \leq p_i \leq 1$.

As for the prey density-dependent factor g_i, it is defined as an increasing function. In the absence of a predator's effect and alternative food choices, this factor becomes directly proportional to the attack rate of prey type i, $g_i \propto C_i$.

The component m_i which, in turns is assumed to be only a predator density-dependent function, serves to capture the effect of facilitation or interference into the predator's capture rate. Thus, in the absence of the afore-cited effects, a constant value or just simply the value 1 is assigned to this factor; $m_i = c$ or $m_i = 1$.

The generalised model proposed by [22] that incorporates facilitation or interference is therefore obtained by considering the generalised form for Type 2 response $F(V_i) = \dfrac{a_i V_i}{1 + \sum_j a_j h_j V_j}$ and replacing the capture rate $a_i V_i$ by the general expression of it, i.e., by C_i; where:

- the selection component $p_i = 1$,
- the prey-dependant factor $g_i = a_i V_i$ and
- the factor defining predator's effects as $m_i = \dfrac{1}{(w_i + P)^{n_i}}$, where the parameters a_i, w_i are positive constant and n_i can be either positive, and in which case we have interference or negative, and in which case facilitation is observed.

From those expressions, it follws that the predator capture rate with respect to each prey i is

$$C_i = \frac{a_i V_i}{(w_i + P)^{n_i}}.$$

This lead to the following predator-dependent generalised functional response;

$$F(V_i) = \frac{\frac{a_i V_i}{(w_i + P)^{n_i}}}{1 + \sum_j h_j \frac{a_j V_j}{(w_j + P)^{n_j}}}. \tag{2.14}$$

When the parameters n_i, w_i are independent of prey type and identical, that is, $n_i = n$ and $w_i = w$ for all the resource types, the Equation (2.14) reduces to

$$F(V_i) = \frac{a_i V_i}{(w + P)^n + \sum_j a_j h_j V_j}.$$

Moreover, if $n = 1$ and there is only one resource type, once finds the Beddington-DeAngelis functional response model

$$F(V) = \frac{aV}{w + P + ahV}$$

and in addition, when the handling time is taken approximately equals to zero ($h \approxeq 0$), this equation collapses into

$$F(V) = \frac{aV}{w + P}$$

which represents the Hassell-Varley response equation [22].

Another class of functional responses dubbed as "ratio dependant functional responses" can be also obtained from the generalised Equation (2.14). Indeed, setting $n_i = 1$ and $w_i = 0$ in (2.14) causes the capture rate to be a function of the ratio of the prey and predator densities ($C_i = a_i \frac{V_i}{P}$) and leads the corresponding feeding rate,

$$F(V) = \frac{aV/P}{1 + ahV/P}$$

for a single-species system. The ratio dependent functional response is viewed as a strong case of the predator-dependent functional response (2.14) [22].

The differentiation or categorisation of functional responses with regard their dependency (prey/predator-dependence or ratio-dependence) raised a simple question; the question of which dependency is the more suitable to describe resource-consumer dynamics. That concern had been an object of a long-standing debate among ecologists and had not found an exact unanimous response. However, some behavioural mechanisms such as switching behaviour, partial preference, and the resource choice maximizing the food intake have been incorporated in the multi-species response to aim for more realism. The next section discusses the effects of such inclusion on resource-consumer dynamics.

2.2 Adaptive Foraging and The Paradigm of Optimal Diet

Since the publication of the Lotka-Volterra predation model, several other models, ecologically more relevant, have emerged. This relevancy is characterized by the inclusion of some realisms or behavioural mechanisms such as "*preference*", "*switching*" and "*diet choice*" observed through experimental investigations and in the field. These behavioural mechanisms constitute somehow evolutionary processes, which make foraging behaviour adaptive according to some environmental changes. Here, we describe the aforementioned behavioural dynamics, review the theory of optimal foraging, cite and discuss some pioneering models incorporating switching mechanism, and resource choice maximizing energy intake. In addition, we will consider the effects of adaptive behaviour on the traditional Hollings' type functional responses.

2.2.1 The Concepts of Preference, Switching, Diet choice and the Theory of Optimal Foraging

The concept behind the terms "preference", "switching" and "Diet choice" are associated with multi-species interactions. A predator feeding on more than one food resources does not attack all the resources haphazardly. Rather, there are some mechanisms guiding the decision to attack that can be explained by the different taste of the prey types, their relative abundance in

the environment, the ability of a predator to detect an encountered individual as a prey, etc.,...

1. Literal definitions

   "Preference" is described as the fact that given an equal abundance of prey species, a predator may still consume one or some of them more frequently than others [26, 27, 22]. While, "switching" refers to the case that the relative intake rate upon a given prey species changes disproportionally when its density changes. That is, the relative number of a prey species in a predator's diet or the number of attacks upon a prey type is disproportionately large when the density of that specific prey is abundant compared to the other available food resources and disproportionately small when that prey species become rarer [26, 27, 13].

   "Diet choice" is a concept related to the availability and presence of alternative food resources for the consumer. Diet choice can be modelled by the selection factor p_i mentioned in the previous section. Preference and switching constitute just outputs of the choices implied by this concept. Performed studies in order to see how diet choice can influence foraging processes have led principally to two different frameworks of representing diet choice into functional responses, one being the classical form where diet choice is represented as a function of resource densities and the other being a resource choice maximizing the food intake. From the latter, optimal foraging theory (OFT) has emerged as the premise of optimal diet models (ODM).

   Originated in the late 60s, the OFT was principally developed from the idea that natural selection of prey or resources/patches might be understood as driven by a tendency, which through evolution, aims to maximize the per capita energy intake rate [30]. That is, given a set of different types of available resources, which types should be included (economically) in the consumer diet.

2. Mathematical formulations

   The terms switching and preference can be evaluated in terms of mathematical expressions. Considering that a predator feeds on n different types of prey, its total resource intake F_t is the summation of the per

capita feeding rate of the different resource types; that is $F_t = \sum_{i=1}^{n} F_i$. Using the population densities V_i, once could have the following relation;

$$\frac{F_i}{F_t} = \frac{\phi_i V_i}{\sum_j \phi_j V_j}, \tag{2.15}$$

where term ϕ_i represents the "preference" with regard to the species of type i and it is generally defined as a normalised term, i.e. $\phi_i < 1$ and $\sum_{j=1}^{n} \phi_j = 1$. Thus, when time scales are taken sufficiently small such that resources densities are relatively constant, the preference toward a species of type i is given as [13, 22]:

$$\phi_i = \frac{F_i/V_i}{\sum_j F_j/V_j}.$$

From the Equation (2.15), it follows that the relative preference of a resource of type i over a resource of j of any given pair of distinct resource types (i, j) is therefore written as;

$$\frac{\phi_i}{\phi_j} = \frac{F_i V_j}{F_j V_i}. \tag{2.16}$$

When $\frac{F_i V_j}{F_j V_i} > 1$, resource type i is said "preferred" over resource type j and the counter intervenes when $\frac{F_i V_j}{F_j V_i} < 1$.

Switching behaviour occurs when the ratio of the per capita feeding rates $\frac{F_i}{F_j} = \frac{\phi_i}{\phi_j}\frac{V_i}{V_j}$ varies disproportionately with the resources density ratio $\frac{V_i}{V_j}$ [26, 27, 22]. That is $\psi_{ij} = \frac{\phi_i}{\phi_j}$, a function of V_i and V_j, respectively, increases or decreases more than linearly as $\frac{V_i}{V_j}$ increases or decreases. The switching can also be qualified as negative; this scenario can be observed by a decreasing behaviour of ψ_{ij} as $\frac{V_i}{V_j}$ increases [13, 4]. For some types of functional responses such as those incorporating interference (2.14), the term ψ_{ij} is a function dependant only on the variable predator density [22]. In such case, where ψ_{ij} is not a function a prey densities V_i, V_j, switching behaviour still occurs, but it is only driven by the predator population density and not of its resources population

densities. From these mathematical formulations, multi-species functional response forms have been classified into three different classes; namely Class 1, Class 2 and Class 3; according to their ability to generate prey-switching. Class 1 gathers functional responses that do not exhibit switching, Class 2 represents those exhibiting "passive switching" and Class 3 where "active switching" is present. The difference between the two latter classes is that switching arises from mechanisms related to single-species responses in Class 2 while in Class 3, switching is due to an active selection in such a way that ψ_{ij} could not be defined from single-species responses' knowledge.

Mathematically, the OFT can be visualised as given a per capita intake rate function R which is dependant on the probability q_i of attacking a prey type i upon encounter or entering a patch i, what values of q_i should maximize R. Considering Holling's type II functional response one possible way of expressing R could be [32]:

$$R = \frac{\sum_{i=1}^{n} q_i \lambda_i e_i}{1 + \sum_{i=1}^{n} q_i \lambda_i h_i}, \tag{2.17}$$

where n represents the number of available types of resources; q_i, the probability of attacking the prey or resource of type i; λ_i the encounter rate with prey type i; e_i the expected net energy gained from an item of prey of type i consumed and h_i the handling time required for an individual prey of type i. Thus, maximizing R with respect to a given q_i returns to looking at how changes in q_i will affect R. This is simply done by differentiating R with respect to q_i.

$$\frac{\partial R}{\partial q_i} = \frac{\partial}{\partial q_i}\left(\frac{\sum_{i=1}^{n} q_i \lambda_i e_i}{1 + \sum_{i=1}^{n} q_i \lambda_i h_i}\right) \tag{2.18}$$

$$= \frac{\partial}{\partial q_i}\left(\frac{q_i \lambda_i e_i + d}{q_i \lambda_i h_i + c}\right) \tag{2.19}$$

$$= \frac{\lambda_i e_i (c + p_i \lambda_i h_i) - \lambda_i h_i (p_i \lambda_i e_i + d)}{(p_i \lambda_i h_i + c_i)^2} \tag{2.20}$$

$$= \frac{\lambda_i e_i c - \lambda_i h_i d}{(p_i \lambda_i h_i + c)^2}; \tag{2.21}$$

where $d = \sum_{j=1; j\neq i}^{n} q_j \lambda_j e_j, \quad c = 1 + \sum_{j=1; j\neq i}^{n} q_j \lambda_j h_j.$

The sign of the equation 2.21 is independent of q_i and therefore the q_i that maximizes R is either the largest or the smallest feasible value of q_i, i.e., either $q_i = 1$ or $q_i = 0$. This constitutes one of the key principle of OFT which is, a resource is either *always taken* or *never taken* (totally ignored) upon encounter [32, 30], there is *no partial preference*. This result is dubbed as the *zero-one* or *bang-bang rule* [32, 23, 10]. So, when does $q_i = 1$ and when does $q_i = 0$? The equation 2.21 provides us with the answer. In fact,

- $q_i = 1$ when $\frac{\partial R}{\partial q_i} > 0$, i.e., $\lambda_i e_i c_i - \lambda_i h_i d_i > 0 \Rightarrow \frac{e_i}{h_i} > \frac{d_i}{c_i}$ and
- $q_i = 0$ when $\frac{\partial R}{\partial q_i} < 0$, i.e., $\lambda_i e_i c_i - \lambda_i h_i d_i < 0 \Rightarrow \frac{e_i}{h_i} < \frac{d_i}{c_i}$.

This constitutes one of the results of OFT: the most profitable resource is always taken upon encounter. The term $\frac{e_i}{h_i}$ measures the profitability of the prey of type i. From this result, [32] presented an optimal diet algorithm that optimally defines when a resource should be included in a consumer's diet.

OFT Algorithm

1- Rank the n different prey types according to their profitability $\frac{e_1}{h_1} > \frac{e_2}{h_2} > \cdots \frac{e_k}{h_k} > \cdots > \frac{e_n}{h_n}$;

2- Add the types to the diet to increase the rank till

$$e_k h_k < \frac{d_k}{c_k}, \quad \text{i.e.,} \frac{e_k}{h_k} < \frac{\sum_{i=1}^{k-1} \lambda_i e_i}{1 + \sum_{i=1}^{k-1} \lambda_i h_i}; \tag{2.22}$$

that is, a type k satisfying the above inequality (2.22) should not be included in the diet and thus $k-1$ constitutes the lowest ranked resource to be considered or including in the diet and if no $k < n$ satisfies this inequality, all the n types are included in the diet.

Based on this algorithm and considering the simplest case, i.e, when $n = 2$, the second type of prey should be considered if and only if

$$\frac{\lambda_1 e_1}{1 + \lambda_1 h_1} < \frac{e_2}{h_2}, \tag{2.23}$$

that is, if considering only the most profitable resource rewards less energy than taking both. Thus, there is a threshold value ($\bar{\lambda}_1$), below which (i.e., $\lambda_1 < \bar{\lambda}_1$), the second prey is always included, and above which (i.e., $\lambda_1 > \bar{\lambda}_1$), the second prey type is always ignored. This value is deduced from the expression (2.23); $\bar{\lambda}_1 = \frac{e_2}{e_1 h_2 - e_2 h_1}$. The threshold value is also called the switching point. However, one should not confuse this with switching property discussed earlier. In fact, this switching point can be just seen as the value at which the consumer behaviour or diet changes. But still, the probability of attacking the most profitable prey remains one. This contradicts the switching property or criterion which states that the ratio of the per capita feeding rates varies disproportionately with the resources density ratio, i.e., disproportionate increase/decrease in the number of attacks upon a resource type when the density of the latter increases/decreases. Briefly put, the zero-one rule stipulates that a prey is taken only when the ratio of benefit and cost is greater than the average one. This result implies that any encountered prey that does not satisfy this rule is ignored. Recent modifications to the classic OFT include the use of decision trees [10] to account for a simultaneous encounter with the prey types; the case of a changed or changing environment [39]; the combination of active switching with maximal feeding [36].

2.2.2 Switching, Maximization of Intake Rate: Effects on Predator-prey Dynamics

Mathematical models for predation systems including switching mechanisms or considering the resource choice maximising the consumer's food intake have been considered by some authors [27, 33, 16, 23, 25, 24, 10, 36].

1. Dynamics of diet models with switching property

   It has been suggested that switching property is a kind of mechanism that can have a stabilizing effect on population dynamic and lead to persistence of the food chain system [26]. This assumption has been discussed further in [27] and has been supported theoretically (see [33], [16]) and empirically (see [9] and references therein).

Systems considering switching mechanisms can be tailored as follow:

$$\begin{cases} \dot{V_1} &= g(V_1) - \dfrac{aV_1}{1+\left(\dfrac{V_2}{V_1}\right)^n}P \\ \\ \dot{V_2} &= g(V_2) - \dfrac{bV_2}{1+\left(\dfrac{V_1}{V_2}\right)^n}P \qquad n \leftarrow 1,2,3,\cdots \\ \\ \dot{P} &= P\left(\dfrac{aV_1}{1+\left(\dfrac{V_2}{V_1}\right)^n} + \dfrac{bV_2}{1+\left(\dfrac{V_1}{V_2}\right)^n}\right) - mP \end{cases} \tag{2.24}$$

Where a, b are respectively the capture or attack rate towards the first and second prey type, n is an exponent describing the strength or intensity of the switching effect (i.e, when n gets large, the predator diet will be mostly constituted with the abundant prey because the probability of attacking that prey type disproportionately increases as n gets large) and

$$g(V_i) = \begin{cases} r_i V_i \quad \text{or} \\ \\ r_i V_i\left(1 - \dfrac{V_i}{K_i}\right) \end{cases}$$

is a function representing the instantaneous growth rate. It should be noted that the functional response in this model is reduced to Holling's type 1 response form in the absence of a second prey type.

The simplest case, i.e., when $n = 1$ and $g(V_i) = rV_i$ was explored by [33]. There, it was shown analytically using Routh-Hurwitz criteria that the system admits a three-coexistence equilibrium which is always stable. However, when the two prey populations have the same intrinsic growth rate ($r_1 = r_2$), the coexistence equilibrium becomes neutral. A more general case $n \leftarrow 1$ to ∞ and the $g(V_i)$ still following exponential growth has been discussed in [16] and it has been shown analytically when $n > 1$, the system possesses a three-coexistence steady state than can be stable, neutral or unstable. More precisely, the system is stable when the prey owning the higher growth rate is

the one affected by a higher predation rate, i.e., three-coexistence equilibrium is always stable if either $r_1 > r_2$ and $a > b$ or $r_2 > r_1$ and $b > a$. Instability is observed when the inequality $1 < \frac{r_1}{r_2} \leq \frac{b}{a}^{n-1}$ holds.

2. Dynamics of classical optimal diet models

Diet models considering the resource maximizing the energy intake have been investigated by several authors, including [32, 23, 25, 24]. In [32], optimality patch selection has been discussed, but this was not explicitly represented as a system of equations to describe or predict the population dynamics of interacting species. Instead, the optimality of the functional response was discussed and conclusions such as when a consumer should leave an entered patch, which patch to enter to maximize the consumer's food intake, etc., have been drawn accordingly.

Explicit models considering the zero-one rule have been discussed in [23, 25, 24] where a system of differential equations with controls was used to describe the dynamics of two prey population and one predator population. The controls define strategies that can enable optimization of the food intake. The studied system is of the Rosenzweig-MacArthur form:

$$\begin{cases} \dot{V}_1 &= r_1\left(1-\dfrac{V_1}{K_1}\right) - \dfrac{q_1\lambda_1}{1+q_1\lambda_1h_1+q_2\lambda_2h_2}P \\ \dot{V}_2 &= r_2\left(1-\dfrac{V_2}{K_2}\right) - \dfrac{q_2\lambda_2}{1+q_1\lambda_1h_1+q_2\lambda_2h_2}P, \qquad \text{where, } \lambda_i = l_iV_i \\ \dot{P} &= P\left(\dfrac{q_1e_1\lambda_1+q_2e_2\lambda_2}{1+q_1\lambda_1h_1+q_2\lambda_2h_2}\right) - mP \end{cases} \tag{2.25}$$

The parameters e_i, q_i, λ_i, l_i represent, respectively, the control parameter (which can be seen as the probability of hunting on V_i), the encounter rate with species V_i, the energy gained per individual of type i consumed, the coefficient of the encounter rate with species of type i. Due to the fact that considering the zero-one rule into functional response results generally into step functions, dynamic of the system (2.25) has been discussed according to three different regions G^1, G^2, G^0

defined as:

$$G^1 = \left\{ (V_1, V_2, P) \in \mathbb{R}^3_+ \mid V_1 < \frac{e_2}{l_1(e_1h_2 - e_2h_1)} \right\},$$

$$G^2 = \left\{ (V_1, V_2, P) \in \mathbb{R}^3_+ \mid V_1 > \frac{e_2}{l_1(e_1h_2 - e_2h_1)} \right\},$$

$$G^0 = \left\{ (V_1, V_2, P) \in \mathbb{R}^3_+ \mid V_1 = \frac{e_2}{l_1(e_1h_2 - e_2h_1)} \right\}.$$

[23] had shown that in G^1, the system (2.25) possesses a three-coexistence equilibrium point

$$E_1 = (V_1^{G_1} > 0, V_2^{G_1} > 0, P^{G_1} > 0)$$

when

$$m < \frac{(e_1K_1 + e_2K_2)l_2}{1 + h_1K_1l_2h_2K_2l_2}$$

and which might be locally stable. While, in G^2, a coexistence steady state

$$E_2 = (V_1^{G_2} > 0, K_2, P^{G_2} > 0)$$

exists provided

$$m < \frac{e_1K_1l_1}{1 + h_1K_1l_1}.$$

Also, E_2 might be globally stable depending on the values of the different parameters of the system. Together with the expressions of $V_1^{G_1}, V_1^{G_2}$ and the conditions of $E_1 \in \mathbb{R}^3_+, E_2 \in \mathbb{R}^3_+$, it is shown that either $E_1, E_2 \in G^1$ or $E_1, E_2 \in G^2$. In addition, it is shown that applying the zero-one rule to the Rosenzweig-MacArthur system 2.25 with two prey populations may not have a stable equilibrium point as in the case of G^1 or G^2 where consumer behaviour can be qualified respectively as generalist -predator feeding on a wide range of species- and specialist (predator specializing on the most profitable resources). In fact, when $r_1 = r_2$ and $l_1 = l_2$, [23] demonstrated that including the second prey type into an unstable system consisting of the most profitable prey and a specialist predator cannot stabilise the system, but instead reduces the amplitude of oscillations, which can be qualified as a partial stabilizing effect. For some parameter values, optimal foraging might destabilize a system with specialist predators when those later became optimal foragers. However, behaving as specialist

on one prey type regardless of their profitability leads to a greater permanence region than foraging optimally on both prey, which in turns admits greater permanence region than a system consisting of a generalist predator which feeds on both resources with $q_i = 1\,(i = 1,2)$ [25].

Moreover, using top-down regulation, [24] explored the effect of OFT on the strength of predator-mediated apparent competition. There it was shown that, contrary to the exclusion of the competitively weaker prey as predicted in non adaptive systems, permanence or coexistence of all species can happen as long as the less profitable prey type is the competitively weaker resource. Besides, maximization of food intake might lead to partial preference. In fact, in G^0 where the zero-one rule is not defined, [23] demonstrated that maximization of the intake rate R leads to higher order system with an approximation of q_2, with $0 < q_2 < 1$, as function depending on the first prey population density and/or predator population density. Thus, in G^0, the shape of the corresponding functional response (predator's response of system (2.25) which is of Holling's type 2) is altered. This confirms Abrams [1] finding which constitutes part of the next section.

2.3 Effects of Adaptive Behaviours on Functional Responses

Proposed models of functional responses can be generally classified into the three traditional Holling's forms type 1, type 2 and type 3. Perhaps due to the simplicity associated with its mathematical expression and positive correlation with laboratory experiments, Type 2 response constitutes the most frequently studied and observed form though predators can change their response form from one type to another. Originally derived based on the assumption that the capture or attack rates, the handling time, the rate of successful and unsuccessful attack are independent of prey densities, Holling's disk equation seems inadequate when it comes to predicting predator responses considering some altered conditions such as the presence of alternative food resources [1] or the fact that digestive pause might not prevent from hunting. This section discusses the effects of the optimal

foraging, and switching behaviour.

2.3.1 Switching, optimal foraging: effects on type 2 response

Since switching and the OFT are concepts related to multi-species system, by which we mean the presence of alternative food sources, we will consider the generalized classical type 2 (4.7) to discuss the effect of foraging optimally and predator switching into a type 2 reposponse.

$$F_i = \frac{a_i V_i}{1 + \sum_j a_j h_j V_j}, \qquad j \leftarrow 1, 2, 3, ..., n, \tag{2.26}$$

where the a_j's and h_j's are constant parameters denoting respectively the attack rate and the handling time per individual prey item of type j. From the OFT, it is possible to have an $a_j = 0$. In fact, the attack rates a_j's can be seen as a constant c multiplied by q_j ($a_j = cq_j$), where q_j represents the probability of attacking a prey of type j following the zero-one rule. Thus the functional response of an optimal forager might be zero at some time interval (when the preferred or most profitable prey density is above its threshold value predicted by the OFT) and generalized type 2 form as equation (4.7) when $a_j = c$; that is when the most profitable prey density is under its threshold value $q_j = 1$ or simply when the prey V_j are included in the predator's diet. Thus, the functional response in term of OFT towards any non most profitable resource is a step function which is not defined at the threshold density of the most profitable resource. Considering the OFT along with an approximation of the q_i's of the less profitable prey at the threshold value of the preferred prey as in [23], the response form becomes a function depending on both prey and predator densities. Besides, even maximization of consumer's fitness, considering the single-species Holling's disk equation results on shapes that differ from the type 2 functional response.
Abrams [1] investigated the effects of optimal foraging or adaptive behaviour on the type 2 response $\frac{cV}{1+chV}$; where V is the prey population density, c the attack rate or capture rate and h the handling time per individual prey. There it was shown that the constant parameters of disk equation vary with prey density when optimization of fitness is taken into account. In general the resulting functional responses from fitness' optimization are of type 2 re-

sponse form, though they diverge from the fixed or constant parameters of disk equation. In fact, maximization of the fitness with respect to handling time h led to a density dependant rate of change of h and a type 2 response form which has the same behaviour as the disk equation at low and high density but differs at intermediate resource density. Besides, maximization of fitness through the successful attack rate c and considering that there is a rate of unsuccessful attack which can be taken as an increasing function of c, result in an expression of c that is prey density dependent; a function of the square root of the resource density. A simple suggestion of the expression of the response in that case resulted in a function which has the same asymptote as the disk equation, but rather increases as a square root of the prey density rather than linearly. Also, the resultant functional response from optimum time spent foraging which maximizes fitness increases as the square root of resource density, and in addition at very high prey density it approaches an asymptote that is related to the expected reproduction, intake rate and the increase of mortality risk.
Existing formulation of switching behaviour into functional responses as in [27, 33, 16, 36] resulted in density dependent attack rates and functional responses that increase more than linearly with resource density. Incorporation of switching mechanisms into the generalized disk equation leads generally to systems with higher order terms which are impossible to analyse analytically. Besides, incorporation of switching property into the disk equation can conserve the same asymptote but the form or type of response might change. In fact, Holling's type 3 response form has been phenomenologically explained by the occurrence of switching behaviour into the predator's feeding strategy.

2.3.2 Satiation effect on type 2 response form

Handling time considered in the derivation of predator responses generally take into account times of different activities from attacking to eating. In the traditional Holling's derivation of type 2 response, handling time is mathematically expressed as the sum of the time spent on attacking a prey item and the time spent on eating that prey, i.e, $h = t_{att} + t_{eat}$, where t_{att}, t_{eat} denote respectively the time spent on attacking (from pursuing to catching) and eating an individual prey item [18]. This formulation received severe

criticisms, including the fact that the predator does not satiate and every predator's attack is effective [19]. To overcome the latter issue, a factor ε representing the efficiency of a predator's capture had been incorporated into the formulation of functional responses such that handling time accounts also for the time wasted into unsuccessful attacks [19], that is

$$h = \frac{t_{att}}{\varepsilon} + t_{eat}. \tag{2.27}$$

Another way is the consideration of fitness' maximization which can lead density dependent formulation of h as in [1]'s paper. However, inclusion of time wasted for unsuccessful attacks into handling time seems to be not enough to describe some field behaviour such that the effect of satiation.
Satiation constitutes another limiting factor of a predator's maximum feeding rate. It has been incorporated into functional response in different ways which have even led to confusion and caused incomprehension. The Gauss-Ivlev response's equation

$$F(V) = V_{max}(1 - exp[-bV]),$$

where b is a hunting success and V_{max} is the maximum predation rate determined by the digestive system, is a typical example of a satiation model even though it does not take account for handling time [19]. Models that include both the satiation effect and handling time are rare. In fact, to deal with the issue of satiation effect in the traditional Holling's disk equation, some authors included digesting time into the handling time equation and this had led to the following equation for handling time;

$$h = t_{att} + t_{eat} + st_{dig}, \tag{2.28}$$

where t_{dig} represents the time period associated with digestion pause and s the satiation factor per individual prey item eaten. Yet, this way of embodying the satiation factor and digestion time into the handling time does not likely distinguish digestion time from handling time. Indeed, handling is an active process, whereas digestion is a background process that might not prevent a predator from searching for or handling of food resources. Jeschke et al. [19] has proposed a mechanistic model (the steady-state satiation) based on the Holling's type 2 predator response, that explicitly discriminates between handling time and digestion time. The steady-state satiation

model is given by:

$$F(V) = \begin{cases} \dfrac{1 + aV(h+c) - \sqrt{1 + aV\left(2(h+c) + aV(h-c)^2\right)}}{2ahcV}, & \text{for, } a, h, c, V > 0 \\ \dfrac{aV}{1 + ahV}, & \text{for, } h > 0, c = 0 \\ \dfrac{aV}{1 + acV}, & \text{for, } h = 0, c > 0 \\ aV, & \text{for, } h = c = 0 \\ 0, & \text{for, } a = 0 \text{ or } V = 0. \end{cases} \tag{2.29}$$

The parameter $a = \beta\gamma\varepsilon$ represents the successful capture rate and it is the product of respectively the encounter rate β, the probability of detection of an encountered prey γ and the attack's efficiency ε. Besides, the handling time h is taken as in the traditional disk equation but in addition, incorporates the efficiency of attack and thus it adopts expression (4.7) form. Satiation is described by $c = st_{dig}$ where s, t_{dig} represent the same components as in equation (4.7a) and it is not confined to handling time. The steady-state satiation is mainly derived by adding a function α representing a search rate in the disk equation and this function depends on another function H (depending on resource density) describing the hunger level. Following some empirical results which state a hyperbolic relation between hunger level and starvation time, Jeschke et al. [19] defined the change in H with respect to time as;

$$\frac{dH(V)}{dt} = \frac{1 - H(V)}{t_{dig}} - sF(V);$$

where $F(V) = \dfrac{\alpha(V)aV}{1 + ah\alpha(V)V}$. The steady-state satiation model 2.29 is obtained by setting $\alpha(V) = H(V)$ and assuming a constant population density, which yielded to $H(V) = 1 - cF(V)$. Also, this formulation can be seen as a general form of type 2 functional response since it encompasses certain characteristics of consumer, namely digestion-limited consumers and handling-limited consumers. From model (2.29) it can be easily seen that the steady-state satiation has the same gradient as the disk equation at low resource density and its asymptote depends on the aforementioned predators'

characteristic. Indeed, when consumers are handling time limited (when $h \geq c$), the steady-state satiation model has the same asymptote as the disk equation, $\frac{1}{h}$; while digestion-limited predators' feeding rate converges to $\frac{1}{c}$ at high resources density.

Chapter 3

An Adaptive Optimal Diet Model

3.1 Introduction

The key element constituting the pillar in the description of consumer-resource interactions is the functional response. Prior studies to quantify the number of captured prey by a predator per unit foraging time resulted in different forms of functional response among which the traditional Holling's types constitute the fundamental. Since Holling's work, considerable advances, including the derivation of a more mechanistic model (the steady-state satiation equation) [19] and the inclusion of more relevant realism (the digestion time, the density dependent rate of capture, the time spent foraging, the handling time, the efficiency of the attacks, the satiation factor, etc.,) [1, 19] have been made on predator's response. Although these contributions can be adequate to describe situations considering adaptive variations in handling time, foraging time, attack rate, and changing environment, the disk equation (type 2 response) remains the most commonly used predator response when it comes to get insights into predator-prey dynamics. This is partly due to the mathematical simplicity associated with the disk equation which, therefore, allows a comprehensive analysis of consumer-resource dynamics. Also, the disk equation described successfully most observed type 2 functional responses by providing better fit to many data sets [1].

Despite these considerable advances made on predator's response, there is still lacking of basics realisms when it comes to functional responses for multi-species system (which happens to be the common case observed in

nature). In fact, apart from the resource choice maximizing the consumer's energy intake and switching behaviour which have been treated independently or separately in the literature, there is no other potent behavioural dynamic reality considered into the formulation of multi-species functional responses. That is, there is no such an explicit version (for multi-species system) of those more realistic or mechanistic functional responses. Besides, another important element, especially when alternative resources are present,i.e., the body size or mass from which depend most of the species' traits or functions is under-represented or absent when studying the dynamics of multi-species systems. In ecological systems, though there are still not well describing factors explaining the selection of certain body sizes, body size remains a prime determiner of interactions. This is because parameters governing exchanges at different trophic levels (exchanges between predators and their prey for instance) are body size dependent [8, 11]. The importance of an individual decision and decisions about prey are all determined by these size relations [8].
Here, we propose a generalized mechanistic resource-consumer model based on the generalised Holling's disk equation and which enables both switching and maximisation of food intake. In addition, our parameterization of the predator handling time, the successful capture rate, the prey per capita rate of increase and the environmental carrying capacity consider predator and/or prey body masses.

3.2 Model Formulation

3.2.1 Model Assumptions and Definition of Variables and Parameters

Like almost any model, the AODM is a compromise between realism and applicability. It is indeed reductive compared to nature, but includes more plausibilities than the multi-species systems explored in [33, 16, 23, 25, 24]. This is because of its simultaneous inclusion of switching behaviour (as defined in [26, 27, 13, 22]) and maximisation of food intake which, to our knowledge, have been discussed separately. Moreover, we choose to define some of the AODM's components as body mass (body size) dependent since body size remains one of the fundamental trait that influences nearly

Table 3.1: AODM Components

Notation	Definition	Range; Unit
	Primary Parameters	
a_i	Search rate: number of encounters between a searching predator and an individual prey of type i	$[0, \infty)$; m^2/s
b_i	Body mass of the prey of type i	$(0, \infty)$, g
b	Body mass of the predator	$(0, \infty)$; g
m	Mortality rate of the predator	$[0, \infty)$; $Inds/s$
q	Allometry exponent	$(-\infty, 1)$; $-$
ℓ	Exponent defining the predator level of adaptiveness	$(-1, \infty)$; $-$
	Secondary Parameters	
c_i	Conversion efficiency with respect to the prey of type i	$(0, 1)$; $-$
r_i	Per capita rate of increase of the prey of type i	$(-\infty, \infty)$,; $Inds/Ind \cdot s$
K_i	Carrying capacity of the prey of type i	$[0, \infty)$; v
h_i	Handling time for a successful attack on a prey of type i	$[0, \infty)$; s
h_i'	Handling time for an unsuccessful attack on a prey of type i	$[0, \infty)$; s
H_i	Average handling time for an attack on prey of type i	$[0, \infty)$; s
γ_i	Rate or efficiency of a successful attack upon a prey of type i	$[0, 1]$; $-$
ϵ	Exponent defining width of the γ_i curve	$[0, \infty)$; $-$
e_i	Profitability of an individual prey of type i	$[0, \infty)$; $-$
	Variables	
V_i	Population density of the prey of type i	$[0, \infty)$; $Inds/m^2$
P	Population density of the predators	$[0, \infty)$; $Inds/m^2$
α_i	Attack probability given an encounter with a prey of type i	$[0, 1]$; $-$

every biological aspect of existing organisms [21, 11]. Besides, we proposed a mechanistic derivation of the predator response. However, the point of the AODM is not to quantitatively describe or predict real multi-species systems dynamics, but rather to get insights on the implications of simultaneously maximizing food intake and allowing for partial preference. For this purpose, we judged not necessary to include too many features in the model, which would render its manipulation cumbersome and therefore uninformative on its dynamic. Table 3.1 describes the different variables and parameters we will be using to construct our model.

To make our model easy to perceive, we have considered the following assumptions:

i) There is a single type of predator and $n \geq 2$ different prey types mixed in the same environment or area (i.e, no patches).

ii) Prey have unlimited resource supply and therefore there is no competition among the prey types except for the apparent competition through the shared predator.

iii) For each prey type, prey population growth is limited by the carrying capacity of the environment and therefore described by the logistic growth equation.

iv) There is no movements in and out (migration) the prey population and prey are randomly distributed in their environment.

v) For each prey of type i, the per capita rate of increase r_i, the carrying capacity K_i, the handling time H_i and the attack efficiency γ_i are functions of the prey and/or predator body size/mass.

3.2.2 Model Development

The derivation of our model response is basically inspired by the work of [17], [27] and [4]. Considering n different types of prey species whose populations are denoted by V_1, V_2, $\cdots$, V_n, we assume a predator allocates all its time to mainly two activities: searching for prey and handling of prey. Thus, either a predator is in a searching state or in a handling state. In the searching state, we assume a predator is looking for a prey in general and once a prey is detected, the predator chooses to attack the specific prey or not according to its profitability. In addition, we assume that not every attack is successful and therefore we include the success rate γ_i given an attack upon a prey of type i. Accordingly, in the handling process, to account for time wasted during unsuccessful attacks in our model, the handling state is divided into two sub-states: successful handling state and unsuccessful handling state. Thus, if T_s denotes the searching time interval, the number of prey of type i captured (successfully attacked) during the search time interval T_s by an individual predator is given by $V_{ic} = a_i \alpha_i \gamma_i V_i T_s$ and the average handling time required for this specific prey type item once attacked (if we ignore the other prey types) could be taken as $H_i = \gamma_i h_i + (1 - \gamma_i)\, h_i'$. Now, if we consider all the n prey types, the total handling time for all the n prey types is given as

$$T_H = \sum_{i=1}^{n} a_i \alpha_i V_i H_i T_s. \tag{3.1}$$

Note that there is no γ_i in equation (3.1) and this is to account for the case of all attacks and, thereby, $a_i\alpha_i V_i T_s$ denotes the number of prey i attacked successfully and unsuccessfully during the search time interval T_s. From equation (3.1), we deduce the expression for the handling time spent on an individual of prey item i captured as

$$T_i = \frac{\sum_{j=1}^{n} a_j\alpha_j V_j H_j}{a_i\alpha_i\gamma_i V_i}$$

and the total time on all the prey of type i captured as;

$$T_{Hi} = \frac{\sum_{j=1}^{n} a_j\alpha_j V_j H_j}{a_i\alpha_i\gamma_i V_i} V_{ic}.$$

Therefore,

$$\begin{aligned}
V_{ic} &= a_i\alpha_i\gamma_i T_s V_i \\
&= a_i\alpha_i\gamma_i (T_t - T_{H_i}) V_i \\
&= a_i\alpha_i\gamma_i (T_t - T_i V_{ic}) V_i \\
\Rightarrow\ & V_{ic}(1 + T_i a_i\alpha_i\gamma_i V_i) = a_i\alpha_i\gamma_i V_i T_t \\
\Rightarrow\ & V_{ic} = \frac{a_i\alpha_i\gamma_i V_i T_t}{1 + T_i a_i\alpha_i\gamma_i V_i} \\
\Rightarrow\ & V_{ic} = \frac{a_i\alpha_i\gamma_i V_i T_t}{1 + \frac{\sum_{j=1}^{n} a_i\alpha_j V_j H_j}{a_i\alpha_i\gamma_i V_i} a_i\alpha_i\gamma_i V_i} \\
\Rightarrow\ & V_{ic} = \frac{a_i\alpha_i\gamma_i V_i T_t}{1 + \sum_{j=1}^{n} a_j\alpha_j V_j H_j}. \qquad (3.2)
\end{aligned}$$

From equation 3.2, we deduce the predator functional response which denotes the number of prey captured per unit time per individual predator as

$$F(V_i) = \frac{a_i\alpha_i\gamma_i V_i}{1 + \sum_{j=1}^{n} a_j\alpha_j V_j H_j}. \qquad (3.3)$$

Considering assumptions i), ii), iii) and iv), our model can be therefore writ-

ten as

$$\begin{cases} \dot{V}_1 &= r_1 V_1 \left(1 - \dfrac{V_1}{K_1}\right) - \dfrac{a_1 \alpha_1 \gamma_1 V_1}{1 + \sum\limits_{j=1}^{n} a_j \alpha_j V_j H_j} P \\ \dot{V}_2 &= r_2 V_2 \left(1 - \dfrac{V_2}{K_2}\right) - \dfrac{a_2 \alpha_2 \gamma_2 V_2}{1 + \sum\limits_{j=1}^{n} a_j \alpha_j V_j H_j} P \\ \vdots & \\ \dot{V}_i &= r_i V_i \left(1 - \dfrac{V_i}{K_i}\right) - \dfrac{a_i \alpha_i \gamma_i V_i}{1 + \sum\limits_{j=1}^{n} a_j \alpha_j V_j H_j} P \\ \vdots & \\ \dot{V}_n &= r_n V_n \left(1 - \dfrac{V_n}{K_n}\right) - \dfrac{a_n \alpha_n \gamma_n V_n}{1 + \sum\limits_{j=1}^{n} a_j \alpha_j V_j H_j} P \\ \dot{P} &= P \sum\limits_{i=1}^{n} \dfrac{c_i a_i \alpha_i \gamma_i V_i}{1 + \sum\limits_{j=1}^{n} a_j \alpha_j V_j H_j} - mP \end{cases} \tag{3.4}$$

Without loss of generality, we will set in our analysis the search rate to be the same for all the prey types; i.e, $\forall i,\ a_i = \mu$, where μ is a constant.

The last assumption of our model states the dependence of some components of the system (3.5) on body masses. In fact, body size/mass largely influences ecological systems at all levels; individual level, population level, community level and ecosystem level [3, 21, 11]. This approach consisting to relate species traits or functions to body mass/size is coined as allometry. According to some allometry scaling models [2, 29, 3, 37, 20, 21], the per capita rate of increase or growth rate r, the carrying capacity K of an organism, handling time h and attack efficiency (rate of a successful attack) are function of body mass. In these relationships, given a species with body size/mass b, its growth rate and carrying capacity are respectively scaled to the power $-1/4$ and $-3/4$. That is, $r = r_0 b^{-1/4}$ and $K = k_0 b^{-3/4}$, where r_0, k_0 are positive constants. These expressions of r and K tell us that, species with smaller body mass/size have a higher rate of increase than larger organisms and the same holds for carrying capacity (see figures 3.2a, 3.2b for illustrations). Besides, handling time is revealed to respectively increase and decrease with increasing prey body mass and increasing predator mass [37, 21], while the attack efficiency follows a hump-shaped relationship with predator-prey body mass ratios [37, 28, 2, 21]. We choose the rate of success-

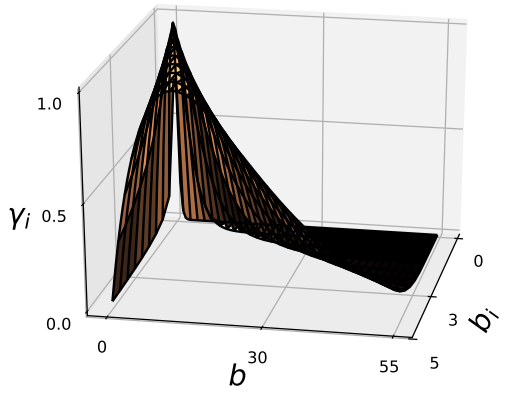
ful attack γ_i of our model to follow the allometry of the attack rate proposed by [28] which is described by a hump-shaped curve as a result of a combination of a power law function and the exponential Ricker function. However, conversely to [28] and [21], we choose the exponential coefficient ϵ to be a function of the power exponent q instead of being a random positive constant. Also, instead of taking the allometry exponent $q < 0$, we set $q \in (-\infty, 1)$ to describe feeding behaviour on small and big prey body sizes.
Thus, we define the function γ_i or $\gamma(b_i)$ as:

$$\gamma_i = b_i^{q-1} b e^{-\epsilon b/b_i} \tag{3.5}$$

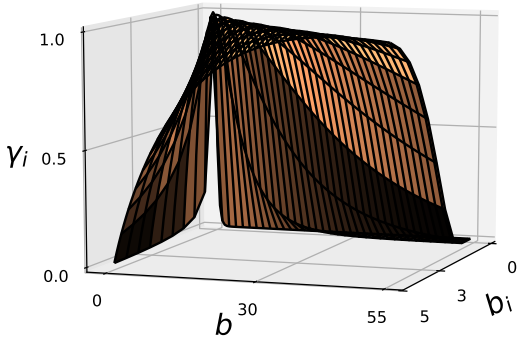
with $\epsilon = \dfrac{1-q}{e} b^{q/(1-q)}$.
This parameterization of γ_i implies that a decreasing in the allometry exponent q decreases the optimal prey body mass catchable by a predator. That is when q goes to $-\infty$, the optimal body mass b_{max} such that the efficiency of a successful attack is at its maximum tends to 0. Figure 3.1 illustrates this scenario. Thus, for predators that exploit prey so small relative to their own size, the exponent q must be negative and for some predators that utilize prey so large (even larger than their own size), q must be taken in $[0, 1)$. From equation (3.5), the optimal prey body mass is obtained by differentiation with respect to b_i and set the resulting equation to zero. After solving this equation for b_i, the optimal prey body mass is given by:

$$b_{max} = \frac{b^{1/1-q}}{e}.$$

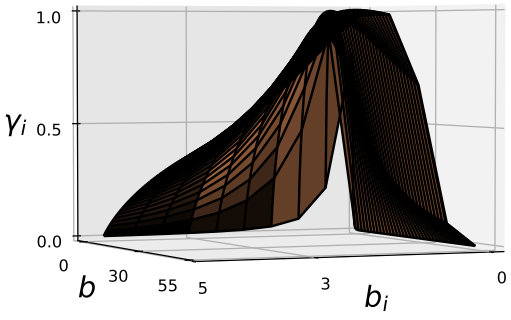
In addition, the parameterization of ϵ constraints γ_i to be in $[0, 1]$. However, once should note that though the function γ_i is continuous on $\mathbb{R}$ and has $[0, 1]$ as range, it is not a probability density function. This because $\int_{\mathbb{R}} \gamma_i db_i \neq 1$.



(a) $q = -0.005$



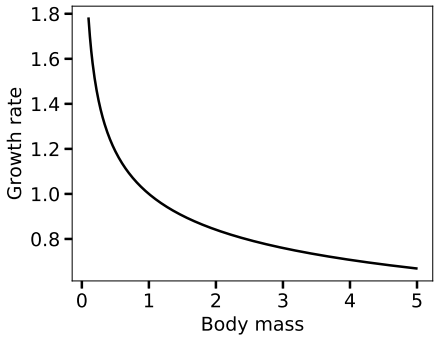
(b) $q = -0.5$



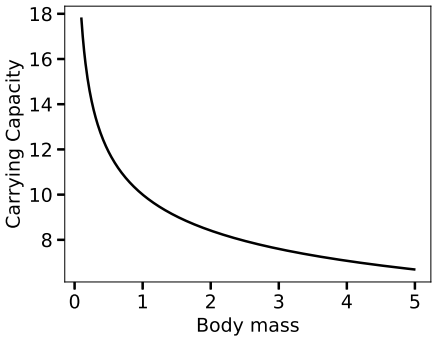
(c) $q = -1.15$

Figure 3.1: Attack efficiency γ_i. The $X-$ axis represents the prey body mass/size (b_i); $Y-$ axis, the predator body mass/size and the $Z-$ axis denotes the function γ_i.

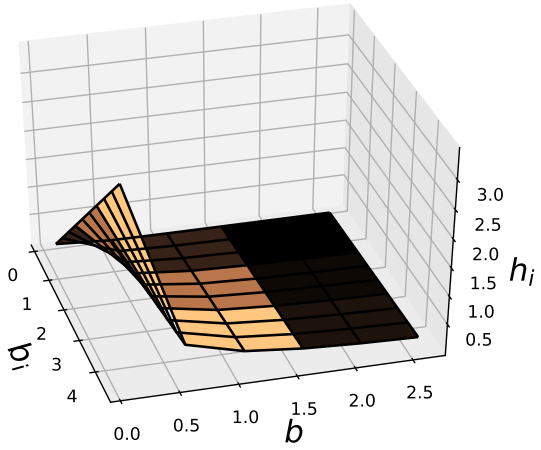
We set the handling time $h_i = h_0 b_i^{c_1} b^{c2}$; $c_1 > 0$, $c_2 < 0$, $h_0 > 0$ according to a prior study by [28]. Note that the constants c_1, c_2 are respectively positive and negative to reflect the fact that an increasing in the prey body mass increases the handling time while an increasing in the predator body mass reduces the handling time. Figure 3.2c illustrates this scenario. The same idea can be applied to the handling time of an unsuccessful attack. In fact, when prey body mass is too small compared to the predator body mass, time spent for an unsuccessful attack can be relatively small because it is easier for the prey to hide or just to be out of sight of the predator. While for a relatively larger prey, the predator might spend more time pursuing or the prey can struggle longer. Thus, in our model we defined the time wasted on unsuccessful attacks (unsuccessful handling time) as $h_i' = h_0' b_i^{c_1} b^{c2}$, with $h_0' < h_0$.



(a)



(b)



(c)

Figure 3.2: In (a): growth rate function; in (b): the carrying capacity and in (c): handling time

We defined the attack probability α_i as follow:

$$\alpha_i = \frac{(e_i V_i)^{\ell_i}}{\sum_{j=1}^{n} (e_j V_j)^{\ell_j}}, \ \ell_i \in (-1, \infty);$$

where $e_i = \frac{b_i \gamma_i}{H_i}$ represents the profitability (the ratio of the benefit of taking prey i over the time required to handle prey i) of the prey i and $\sum_{i=1}^{n} \alpha_i =$

1. This frequency and profitability-dependant definition of α_i is to shape both the idea of optimal diet choice and switching behaviour. In fact, there are several reasons that can cause a predator to prefer a specific prey type over others. Some of these reasons include the relative density of each prey species in the system and their profitability. For instance the most abundant prey can be more preferred because predators might forget that the rarer prey is edible [27] or the environment may dispose refuge places which can then provide more safety for prey at low density. Thus, we assume that the predator searches randomly and encounters the different prey species in proportion to their abundance and that any encountered prey has some probability of being taken which is greater if the encountered prey is the most abundant type and/or is the most profitable.
In system (3.5), we choose the conversion efficiency of an individual prey item of type i captured to be $c_i = cb_i/b$; where c is a positive constant such that $0 < \frac{cb_i}{b} < 1$. This, is not a general rule and therefore can be replaced by any other value in $(0, 1)$. However, studies relating body size to predator-prey dynamics revealed that the conversion efficiency scales with the ratio of the prey and predator body sizes [38].

3.3 AODM Properties

This section's concern is to prove that our model, represented by the system of equations (3.5), is both mathematically and biologically plausible. For this reason, existence, uniqueness and boundedness of solutions have to be ascertained. Besides, we claim that for certain values of ℓ_i the AODM admits switching property as defined by [27] and/or rank switching property as defined by [4].

3.3.1 Existence, Uniqueness and Boundedness

The right-hand sides of the system (3.5) are differentiable for all $V \in \mathbb{R}_+^{n+1}$ and the partial derivatives are continuous on $\mathbb{R}_+^{n+1}$. Therefore, the right-hand sides of system (3.5) are Lipschitz continuous and in consequence, given an initial condition, solution to system (3.5) exists and is unique.
Theorem 1. Solutions to system (3.5) are bounded.
Proof. Let $W(t) = P(t) + \sum_i^n V_i$. Differentiating with respect to t lead to:

$$
\begin{aligned}
\frac{dW(t)}{dt} &= \frac{dP(t)}{dt} + \frac{d}{dt}\sum_{i=1}^{n} V_i \\
&= \frac{dP(t)}{dt} + \sum_{i=1}^{n}\frac{dV_i}{dt} \\
&= \sum_{i=1}^{n}\frac{cb_i a_i \alpha_i \gamma_i V_i P}{1+\sum_{j=1}^{n} a_j \alpha_j V_j H_j} - mP + \sum_{i=1}^{n}\left(r_i V_i\left(1-\frac{V_i}{K_i}\right) - \frac{a_i \alpha_i \gamma_i V_i P}{1+\sum_{j=1}^{n} a_j \alpha_j V_j H_j}\right) \\
&= \sum_{i=1}^{n}\frac{a_i \alpha_i \gamma_i V_i P}{1+\sum_{j=1}^{n} a_j \alpha_j V_j H_j}(c_i - 1) - mP + \sum_{i=1}^{n} r_i V_i\left(1-\frac{V_i}{K_i}\right) \\
&\leq \sum_{i=1}^{n} r_i V_i\left(1-\frac{V_i}{K_i}\right) - mP \\
&\leq \sum_{i=1}^{n} r_i V_i - \sum_{i=1}^{n}\frac{r_i V_i^2}{K_i} - mP \\
&\leq \sum_{i=1}^{n} r_i V_i - mp \\
&\leq \sum_{i=1}^{n} RA - mW(t) + \sum_{i=1}^{n} mV_i \\
&\leq nAR + nmA - mW(t) \\
&\leq nA(R+m) - mW(t) \qquad (3.6) \\
&\leq 2ndA - mW(t) \qquad (3.7)
\end{aligned}
$$

where $A = \max\{P(0), K_i, V_i(0),\ i \leftarrow 1, 2, \cdots, n\}$, $d = \max\{R, m, 1\}$, $R = \max\{r_i,\ i \leftarrow 1, 2, \cdots, n\}$.
From inequality (3.6), we have $\frac{dW(t)}{dt} + mW(t) \leq 2nA$ and using the technique of an integrating factor we obtain for all $t \geq T \geq 0$;

$$
\begin{aligned}
\int_T^t d(e^{ms}W(s)) &\leq \int_T^t e^{ms} 2ndA\,ds \\
&\Longrightarrow W(t) \leq 2ndA - [2ndA - W(T)]\, e^{m(T-t)}.
\end{aligned}
$$

Thus, if $T = 0$, we arrive to the following inequality;

$$
W(t) \leq 2ndA - [2ndA - W(0)]\, e^{-mt} \qquad (3.8)
$$

Since $2ndA - W(0) \geq 0$, we have $W(t) \leq 2ndA$, $\forall t \geq 0$. This, implies that all species are bounded for any initial value in $\mathbb{R}_+^{n+1}$. Therefore, according to the above theorem there exists $(\vartheta_1, \vartheta_2, \cdots, \vartheta_{n+1}) \geq 0_{n+1}$ such that $\Omega(V_1(0), V_2(0), \cdots, V_n(0), P(0)) \subset \Re_+^{n+1}$, where $\Omega\left(V_1(0), V_2(0), \cdots, V_n(0), P(0)\right)$ is the limit set of the orbit initiating at $(V_1(0), V_2(0), \cdots, V_n(0), P(0))$ and $\Re_+^{n+1} = \{(x_1, x_2, \cdots, x_{n+1}) : 0 \leq x_1 \leq \vartheta_1, 0 \leq x_2 \leq \vartheta_2, \cdots, 0 \leq x_n \leq \vartheta_n, 0 \leq x_{n+1} \leq \vartheta_{n+1}\} \forall\ (V_1(0), \cdots, V_n(0), P(0)) \geq 0$. Thus, solutions to the model defined by system (3.5) are bounded.

3.3.2 Verification of the Switching Criterion

Proposition: System (3.5) admits switching property for $\ell \in I = (-1, 0) \cup (0, \infty)$.

Proof Let's $i, j \in \{1, 2, \cdots, n\}, i \neq j$ represent two different types of prey species. Therefore, we have:

$$\begin{aligned}
\frac{F(V_i)}{F(V_j)} &= \frac{\dfrac{a_i\alpha_i\gamma_i V_i}{1 + \sum\limits_{k=1}^{n} a_k\alpha_k V_k H_k}}{\dfrac{a_j\alpha_j\gamma_j V_j}{1 + \sum\limits_{k=1}^{n} a_k\alpha_k V_k H_k}} \\
&= \frac{a_i\alpha_i\gamma_i V_i}{a_j\alpha_j\gamma_j V_j} \\
&= \frac{a_i \dfrac{(e_i V_i)^{\ell_i}}{\sum\limits_{k=1}^{n} (e_k V_k)^{\ell_k}}\gamma_i V_i}{a_j \dfrac{(e_j V_j)^{\ell_j}}{\sum\limits_{k=1}^{n} (e_k V_k)^{\ell_k}}\gamma_j V_j} \\
\frac{F(V_i)}{F(V_j)} &= \frac{a_i (e_i V_i)^{\ell_i}\gamma_i V_i}{a_j (e_j V_j)^{\ell_j}\gamma_j V_j}.
\end{aligned}$$

Thus, switching behaviour occurs in the model (3.5) when $\ell_i \neq 0$, $\forall i \in I$. The exponent ℓ_i measures the predator level of adaptiveness; a value of 0 implies a random foraging (i.e, no switching), the predator exhibits just a preference for the easier catchable resource type and, therefore, the probability of attacking any encountered prey is the same for all the n prey types

and it is given by $\alpha_i = 1/n, \forall i$. Moreover, when $\forall\, i$, $\ell_i = m \in (-1, 0)$ and $\forall\, i$, $\ell_i = m \in (0, \infty)$, we have respectively negative and positive prey switching. We also claim that the AODM response is a generalized functional response. In fact, though it is not possible with our current formulation of α_i, γ_i and H_i to recover most of the recent formulation of functional responses with our AODM's response (equation (3.3)), it should noted that the traditional Holling's types and the Type 3 formulation by [4] can be easily retrieved from equation (3.3) as follow:

$$F(V_i) = \begin{cases} \dfrac{\widetilde{a}_i \gamma_i V_i}{1 + \sum\limits_{j=1}^{n} \widetilde{a}_j H_j V_j}; \quad \widetilde{a}_i = a_i/n, \quad \text{when } \ell_i = 0 \ \forall i \\ \dfrac{\widetilde{a}_i \gamma_i V_i^m}{1 + \sum\limits_{j=1}^{n} \widetilde{a}_j H_j V_j^m}; \quad \widetilde{a}_i = \dfrac{a_i e_i^l}{\sum\limits_{j=1}^{n} (e_j V_j)^l}; \quad m = l + 1, \quad \text{when } \ell_i = l \ \forall i \\ \dfrac{\widetilde{a}_i \gamma_i V_i^{m_i}}{1 + \sum\limits_{j=1}^{n} \widetilde{a}_j H_j V_j^{m_j}}; \quad \widetilde{a}_i = \dfrac{a_i e_i^{\ell_i}}{\sum\limits_{j=1}^{n} (e_j V_j)^{\ell_j}}; \quad m_i = \ell_i + 1. \end{cases} \tag{3.9}$$

The first equation of system (3.9) describes the Holling's type 2 response for a multi-species system and in a case of a single prey type, this equation drops to the classical Holling's disk equation. The second equation defines the type 3 Holling's response form for multi-species system. Besides, when $H_i = 0 \ \forall i$ and $e_i = b_i \gamma_i$, this second equation turns to the type 1 form defined by [33] (that verifies switching property).

Chapter 4

AODM Dynamics

4.1 Analytical Results

The dynamic of the system (3.5) with only two distinct prey populations has five variables (three state variables and two secondary variables), twenty-five parameters (eight primary parameters and seventeen secondary parameters). This makes the assessment of analytical local stability investigation unwieldy. Also, resorting to the non-dimensional form of the system (3.5) is not as helpful as much because it is not reducing considerably the number of parameters. Thus, performing detailed stability analysis of the three state variables is cumbersome and therefore, in this section, we will only focus on investigating analytically the simplest case of our model; that is when the switching exponents $\ell_i = 0$, $\forall i$ and give a brief analytical detail when $\ell_i > 0$. Without lost of generality, in the rest part of this project, we assume that $\ell_i = \ell$, $\forall i$ for some $\ell \in \mathbb{R}_+$.

4.1.1 Equilibria

When $\ell = 0$ and we only consider two prey types, the model (3.5) can be rewritten as:

$$\begin{cases} \dot{V}_1 &= r_1 V_1 \left(1 - \dfrac{V_1}{K_1}\right) - \dfrac{\beta_1 V_1}{1 + H_1 V_1 + H_2 V_2} P \\ \dot{V}_2 &= r_2 V_2 \left(1 - \dfrac{V_2}{K_2}\right) - \dfrac{\beta_2 V_2}{1 + H_1 V_1 + H_2 V_2} P \\ \dot{P} &= P \dfrac{c_1 \beta_1 V_1 + c_2 \beta_2 V_2}{1 + H_1 V_1 + H_2 V_2} - mP; \end{cases} \tag{4.1}$$

where $\beta_i = \frac{1}{2} a_i \gamma_i$ and $H_i = \frac{1}{2} a_i \left(\gamma_i h_i + (1 - \gamma_i) h_i'\right)$. The factor $1/2$ comes from the fact that when $\forall j \, \ell_j = 0$ then $\alpha_i = \dfrac{(e_i V_i)^{\ell_i}}{\sum_{j=1}^{n} (e_j V_j)^{\ell_j}} = \dfrac{1}{n}$. Note that we cannot solve analytically system (4.1) and therefore to access its dynamical behaviour, we resort to the analysis of its equilibria via linearisation.
Solving the right-hand side of the system (4.1) equals to zero gives five equilibrium points; $E_0 = (0, 0, 0), E_{12} = (K_1, K_2, 0), E_{13} = (V_1^{13}, 0, P^{13}), E_{23} = (0, V_2^{23}, P^{23})$ and $E_{123} = (V_1^*, V_2^*, P^*)$; where:

$$V_1^{13} = \frac{m}{c_1 \beta_1 - m H_1},$$

$$P^{13} = \frac{r_1 c_1 \left[K_1 (c_1 \beta_1 - m H_1) - m\right]}{K_1 (c_1 \beta_1 - m H_1)^2},$$

$$V_1^{23} = \frac{m}{c_2 \beta_2 - m H_2},$$

$$P^{23} = \frac{r_2 c_2 \left[K_2 (c_2 \beta_2 - m H_2) - m\right]}{K_2 (c_2 \beta_2 - m H_2)^2},$$

$$V_1^* = \frac{K1 (c_2 \beta_2 - m H_2)(\beta_{21} - r_{21}) + m r_{21} K_{12}}{\beta_{21} (c_2 \beta_2 - m H_2) + K_{12} r_{21} (c_1 \beta_1 - m H_1)},$$

$$V_2^* = \frac{\beta_{21} m + K1 (c_1 \beta_1 - m H_1)(r_{21} - \beta_{21})}{\beta_{21} (c_2 \beta_2 - m H_2) + K_{12} r_{21} (c_1 \beta_1 - m H_1)},$$

$$P^* = \frac{r_1 (K_1 - V_1^*)(1 + H_1 V_1^* + H_2 V_2^*)}{\beta_1 K_1},$$

with $\beta_{ij} = \frac{\beta_i}{\beta_j}$, $r_{ij} = \frac{r_i}{r_j}$, $K_{ij} = \frac{K_i}{K_j}$.
The equilibrium points E_{13} and E_{23} are strictly positive (i.e., $V_1^{13} > 0$, $P^{13} > 0$ and $V_1^{23} > 0$, $P^{23} > 0$) or feasible provided respectively $\frac{c_1\beta_1 K_1}{1 + H_1 K_1} > m$ and $\frac{c_2\beta_2 K_2}{1 + H_2 K_2} > m$. This implies that the predator mortality rate should be less than the profitability of a prey type i (that is $m < \frac{c_1}{H_1}$) for each of the equilibria E_{i3} to be feasible. These equilibria describe the case when only one prey type co-exists with the predator population.

Equilibrium E_{123} is feasible if the following inequalities are satisfied:

1. $K1(c_2\beta_2 - mH_2)(\beta_{21} - r_{21}) + mr_{21}K_{12} > 0$ and $\beta_{21}(c_2\beta_2 - mH_2) + K_{12}r_{21}(c_1\beta_1 - mH_1) > 0$ or $K1(c_2\beta_2 - mH_2)(\beta_{21} - r_{21}) + mr_{21}K_{12} < 0$ and $\beta_{21}(c_2\beta_2 - mH_2) + K_{12}r_{21}(c_1\beta_1 - mH_1) < 0$

2. $\beta_{21}m + K1(c_1\beta_1 - mH_1)(r_{21} - \beta_{21}) > 0$ and $\beta_{21}(c_2\beta_2 - mH_2) + K_{12}r_{21}(c_1\beta_1 - mH_1) > 0$ or $\beta_{21}m + K1(c_1\beta_1 - mH_1)(r_{21} - \beta_{21}) < 0$ and $\beta_{21}(c_2\beta_2 - mH_2) + K_{12}r_{21}(c_1\beta_1 - mH_1) < 0$

In general, for n prey types, we have $\left(3 + \sum_{k=1}^{n-1} \binom{n}{k}\right)$ equilibria. These equilibria are the null equilibrium; the equilibrium that all prey are at their carrying capacity in the absence of the predator population; the all species equilibrium where all the species coexist and the different k-species equilibria ($1 \leq k \leq n-1$) where we have coexistence of k prey types and the predator population. Thus, for any $k \in [1, n-1]$, there is $\binom{n}{k}$ k-species equilibria. For $n > 2$ prey types, analytical analysis of our AODM or any predator-prey model with a type 2 response is cumbersome if not impossible.

4.1.2 Bifurcation Analysis

The linearisation matrix of our model (4.1) is given by:

$$
\begin{bmatrix}
\frac{r_1}{K_1}(K_1 - 2V_1) - \frac{\beta_1 P(1 + H_2V_2)}{(1 + H_1V_1 + H_2V_2)^2} & \frac{\beta_1 H_2 V_1 P}{(1 + H_1V_1 + H_2V_2)^2} & \frac{\beta_1 V_1}{1 + H_1V_1 + H_2V_2} \\
\frac{\beta_2 H_1 V_2 P}{(1 + H_1V_1 + H_2V_2)^2} & \frac{r_2}{K_2}(K_2 - 2V_2) - \frac{\beta_2 P(1 + H_1V_1)}{(1 + H_1V_1 + H_2V_2)^2} & \frac{\beta_2 V_2}{1 + H_1V_1 + H_2V_2} \\
\frac{P\,(\beta_1 c_1 + \beta_1 c_1 H_2V_2 - \beta_2 c_2 H_1V_2)}{(1 + H_1V_1 + H_2V_2)^2} & \frac{P\,(\beta_2 c_2 + \beta_2 c_2 H_1V_1 - \beta_1 c_1 H_2V_1)}{(1 + H_1V_1 + H_2V_2)^2} & \frac{\beta_1 c_1 V_1 + \beta_2 c_2 V_2}{(1 + H_1V_1 + H_2V_2)} - m
\end{bmatrix} \tag{4.2}
$$

Thus, the Equilibrium E_0 has $\lambda_1 = r_1$, $\lambda_2 = r_2$ and $\lambda_3 = -m$ as eigenvalues and it is therefore an unstable node since the r_i are positive parameters.

E_{12} has $\lambda_1 = -r_1, \lambda_2 = -r_2$, and $\lambda_3 = \dfrac{c_1\beta_1 K1 + c_2\beta_2 K_2 - mH_1K_1 - mH_2K_2 - m}{1 + H_1K_1 + H_2K_2}$ and it is locally stable if

$$m > \frac{c_1\beta_1 K_1 + c_2\beta_2 K_2}{1 + H_1K_1 + H_2K_2}.$$

Eigenvalues of E_{i3} give complex expressions that we are not able to analyse their stability. To access the local stability of the E_{123} is also cumbersome because of its enormous expression. To reduce this complexity, let's assume that prey 1 and prey 2 have the same per-capita growth rate and the same a_i, γ_i. Thus, $r_{12} = r_{21} = 1$ and $\beta_{12} = \beta_{21} = 1$ and therefore the components of E_{123} are reduced to:

$$V_1^* = \frac{mK_1}{K_2(c_2\beta_1 - mH_2) + K_1(c_1\beta_1 - mH_1)},$$

$$V_2^* = \frac{mK_2}{K_2(c_2\beta_1 - mH_2) + K_1(c_1\beta_1 - mH_1)},$$

$$P^* = \frac{\beta_1 (c_1K_1 + c_2K_2) [K_2 (c_2\beta_1 - mH_2) + K_1 (c_1\beta_1 - mH_1) - m]}{[K_2(c_2\beta_1 - mH_2) + K_1(c_1\beta_1 - mH_1)]^2}.$$

In this case, E_{123} is strictly positive if

$$m < \frac{\beta_1(H_1K_1 + H_2K_2)}{1 + H_1K_1 + H_2K_2}$$

and following [23] we deduce the eigenvalues of E_{123}:

$$\lambda_1 = \frac{m\beta_1}{m(H_1K_1 + H_2K_2) - \beta_1(c_1K_1 + c_2K_2)},$$

$$\lambda_2 = \frac{\beta_1 B - \sqrt{(\beta_1 B)^2 + 4\beta_1 AD}}{2A},$$

$$\lambda_3 = \frac{\beta_1 B + \sqrt{(\beta_1 B)^2 + 4\beta_1 AD}}{2A};$$

where

$$A = \beta_1 (c_1K_1 + c_2K_2) (c_1\beta_1K_1 + c_2\beta_1K_2 - mH_1K_1 - mH_2K_2),$$

$$B = -m \left((c_1K_1 + c_2K_2)(1 - H_1K_1 - H_2K_2) + \frac{m}{\beta_1}(H_1K_1 + H_2K_2)(1 + H_1K_1 + H_2K_2) \right),$$

$$D = m\left(-c_1\beta_1K_1 - c_2\beta_1K_2 + m(1 + H_1K_1 + H_2K_2)\right)\left(c_1K_1 + c_2K_2 - \frac{m}{\beta_1}(H_1K_1 + H_2K_2)\right).$$

E_{123} is locally stable if all the real part of λ_1, λ_2 and λ_3 are all negative. Thus, we have:

$$\begin{aligned} \Re(\lambda_1) < 0 \quad &\Rightarrow \quad m(H_1K_1 + H_2K_2) - \beta_1(c_1K_1 + c_2K_2) < 0 \\ &\Rightarrow \quad m < \frac{\beta_1(c_1K_1 + c_2K_2)}{H_1K_1 + H_2K_2} \end{aligned} \tag{4.3}$$

For λ_2 and λ_3 to be negative, let's assume that they are complex conjugates. This can only happen if $\sqrt{(\beta_1B)^2 + 4\beta_1AD}$ is a pure imaginary number; that is when $(\beta_1B)^2 < -4\beta_1AD$. This implies $\beta_1 < \frac{-4AD}{B^2}$. Since $\beta_1 > 0$ and $m < \frac{\beta_1(c_1K_1 + c_2K_2)}{H_1K_1 + H_2K_2}$ from 4.3 (which implies $A > 0$) we have;

$$\beta_1 < \frac{-4AD}{B^2} \Rightarrow D < 0$$

and

$$D < 0 \Rightarrow m < \frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2}.$$

Now that we have the different conditions for λ_2 and λ_3 to be complex, E_{123} can only be locally stable if $\frac{\beta_1B}{2A} < 0$; that is when $B < 0$ since $A > 0$ and $\beta_1 > 0$. Thus, $B < 0$ implies

$$m > \frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(H_1K_1 + H_2K_2)(1 + H_1K_1 + H_2K_2)}.$$

Since

$$\frac{\beta_1(c_1K_1 + c_2K_2)}{H_1K_1 + H_2K_2} > \frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2}$$

and

$$\frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2} > \frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(1 + H_1K_1 + H_2K_2)(H_1K_1 + H_2K_2)};$$

it turns out λ_2 and λ_3 have negative real part (i.e, E_{123} is locally stable) if

$$\frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(1 + H_1K_1 + H_2K_2)(H_1K_1 + H_2K_2)} < m < \frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2}. \tag{4.4}$$

In the other hand, if we assume that λ_2 and λ_3 are real numbers

(i.e, $\beta_1 < \frac{-4AD}{B^2}$); for E_{123} to be locally stable λ_2 and λ_3 should be negative. From the inequality (4.3), it follows that $\lambda_3 \geq \lambda_2$. Therefore E_{123} is locally stable if $\lambda_3 < 0$.

$$\begin{aligned} \lambda_3 < 0 \quad &\Leftrightarrow \quad \frac{\beta_1 B + \sqrt{(\beta_1 B)^2 + 4\beta_1 AD}}{2A} < 0 \\ &\Rightarrow \quad \beta_1 B + \sqrt{(\beta_1 B)^2 + 4\beta_1 AD} < 0, \quad \text{since } A > 0 \\ &\Rightarrow \quad B < 0 \quad \text{and} \quad D < 0. \end{aligned} \tag{4.5}$$

Thus, in conclusion, E_{123} is locally stable provided one of the following conditions is satisfied:

1. $\beta_1 > \frac{-4AD}{B^2}$ and
$$\frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(1 + H_1K_1 + H_2K_2)(H_1K_1 + H_2K_2)} < m < \frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2}.$$

2. $\beta_1 < \frac{-4AD}{B^2}$ and
$$\frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(1 + H_1K_1 + H_2K_2)(H_1K_1 + H_2K_2)} < m < \frac{\beta_1(c_1K_1 + c_2K_2)}{1 + H_1K_1 + H_2K_2}.$$

If $m \leq \frac{\beta_1(c_1K_1 + c_2K_2)(H_1K_1 + H_2K_2 - 1)}{(1 + H_1K_1 + H_2K_2)(H_1K_1 + H_2K_2)}$ (i.e, $\beta_1 B2A \geq 0$), system (4.1) goes
under Hopf bifurcation and a stable limit cycle may appear around E_{123}.

4.2 Numerical Results

In this section, the global dynamical behaviour of the system (3.5) with $n = 2$ is investigated numerically. A numerical integration of the system (3.5) is carried out for the various choices of biologically feasible parameter values:

- $\ell_i \in [0, 20]$,
- $K_0 \in [2, 18]$,
- $q \in [-3, 0.15]$,
- $m \in [0.1, 0.65]$,
- $c_0 \in [0.15, 0.975]$,

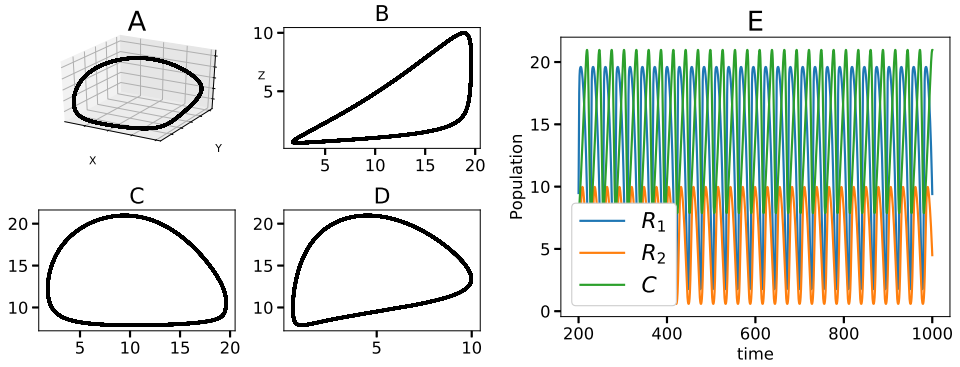
- $h_0 \in [0.2, 2.5]$

We investigated the model system behaviour by looking at the phase plane diagrams while varying the aforementioned parameters. The Python ode integrator (odeint) is used to solve numerically our system. Note that we deliberately choose not to vary the b_i because its effect can be derived from the change in the allometry exponent q. In fact, changing q alters the effectiveness of an attack's success and optimal body mass b_{max} (the body mass for which $\gamma(b_{max}) = 1$). In the following part of this section, the X, Y, Z-axes denote respectively the prey 1, prey 2 and predator population density; sub-figure B denotes the phase portrait in the $XY-$plane; sub-figures C, and D represent respectively the phase portrait in the $XZ-$plane and $YZ-$plane.

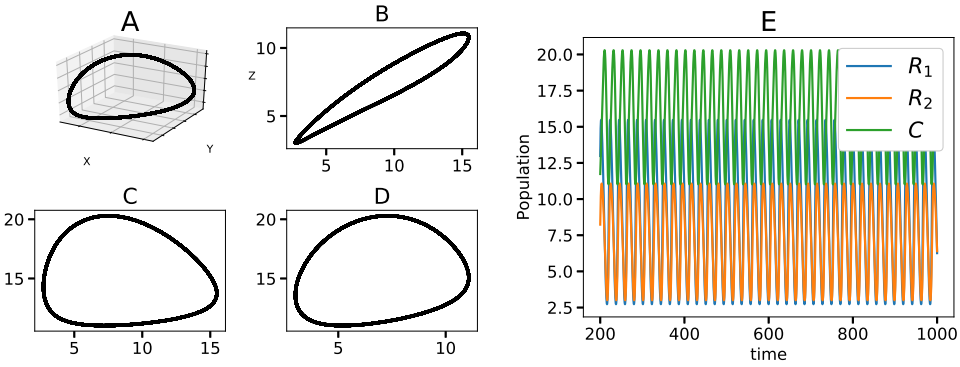
4.2.1 Effects of Prey Components

In this section, the effects of the different parameters present in the equation describing the prey population growth rate, namely the switching exponent ℓ_i, the handling time H_i, the allometry exponent q, and the carrying capacity K_i are explored. We consider two prey populations with different characteristics, so that the predator's attack probability will be both based on the prey profitability and density.

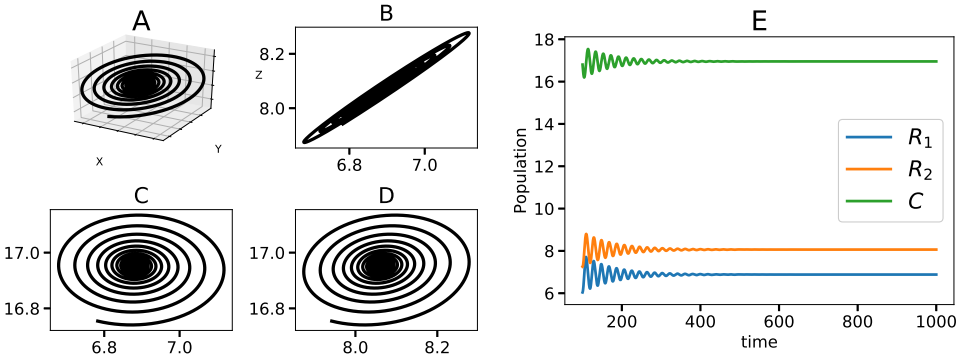
1. Effects of the switching exponent



(a) A_1 (b) A_2



(c) B_1 (d) B_2

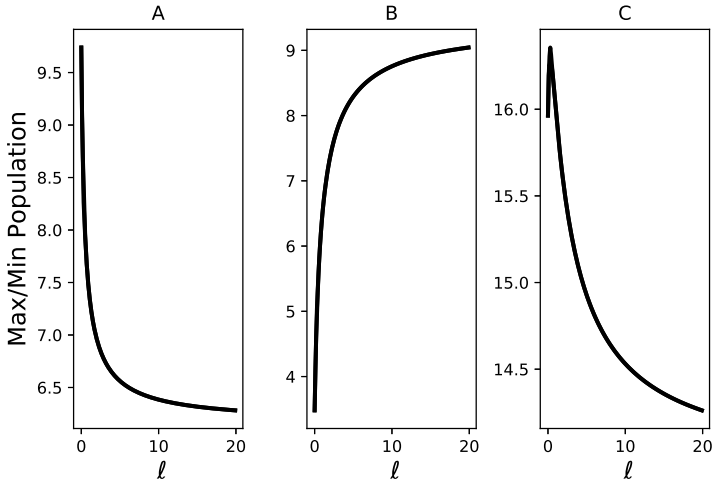


(e) C_1 (f) C_2

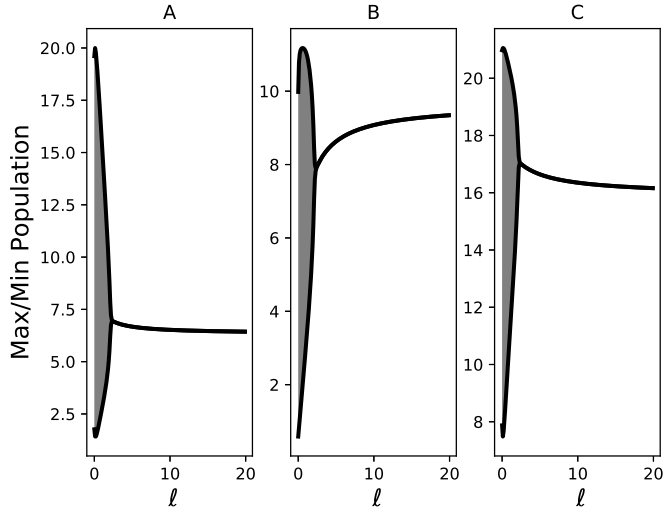
Figure 4.1: Predator-Prey dynamics and phase portrait according to the switching ℓ. The left-hand side of each sub-plot represents the phase portrait of the time series on the right side. In A_{1-2}, $\ell = 0$; in B_{1-2}, $\ell = 1$ and in C_{1-2}, $\ell = 2.75$. In all the figures, $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $K_{12} = [25, 15]$, $h_0 = 1.25$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$.

Model system (3.5) shows rich dynamics with respect to varying the

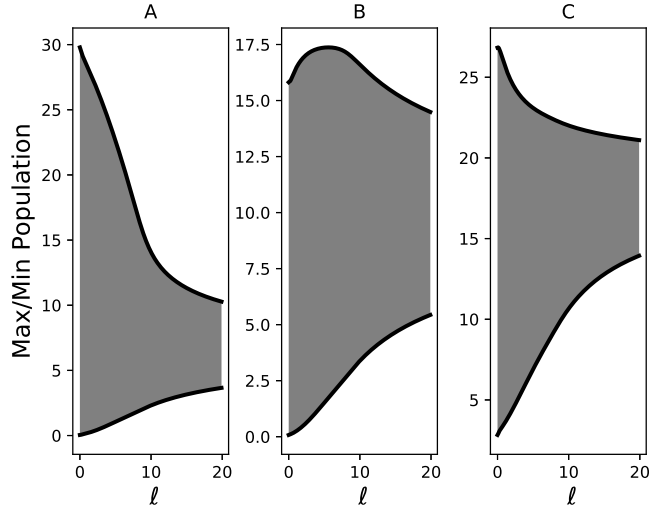
switching exponent ℓ (which also leads to optimal diet choice for larger values). From figure 4.1, increasing ℓ mainly leads to the decrease of the amplitude of oscillations. We remark that random foraging (figure 4.1a) presents larger oscillations than when $\ell > 0$. The parameters' values with respect to figure 4.1 give respectively $(\lambda_1 \simeq -0.395, \lambda_2 \simeq 0.023 - 0.265i, \lambda_3 \simeq 0.023 + 0.265i)$; $(\lambda_1 \simeq -1.134, \lambda_2 \simeq 0.005 - 0.31i, \lambda_3 \simeq 0.005 + 0.31i)$ and $(\lambda_1 \simeq -3.058, \lambda_2 \simeq -0.012 - 0.325i, \lambda_3 \simeq -0.012 + 0.325i)$ as eigenvalues. The system oscillates around the point $V \simeq (10.688, 5.283, 14.425)$ when $\ell = 0$ and around respectively the points $V \simeq (9.185, 7.038, 15.657)$, $V \simeq (6.882, 8.063, 16.953)$ when $\ell = 1, 2.75$. Thus varying the switching exponent can lead both to stability and instability. In fact, when $\ell = 0$ and $\ell = 1$ we have a repelling saddle focus (4.1a and 4.1c) since one of the eigenvalues is a negative real and two are complex conjugate with positive real part. Increasing ℓ to 2.75 gives an attracting focus (see figure 4.1e), i.e., all the eigenvalues have negative real parts. The general effect of the predator's adaptiveness level to the AODM model can be resumed according to the bifurcation diagrams 4.2.



(a)



(b)



(c)

Figure 4.2: Bifurcation diagrams with respect to the changing ℓ. In (a): $K_{12} = [22, 13]$; (b): $K_{12} = [25, 15]$ and in (c): $K_{12} = [32, 18]$. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $h_0 = 1.25$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$.

2. Effects of the carrying capacity

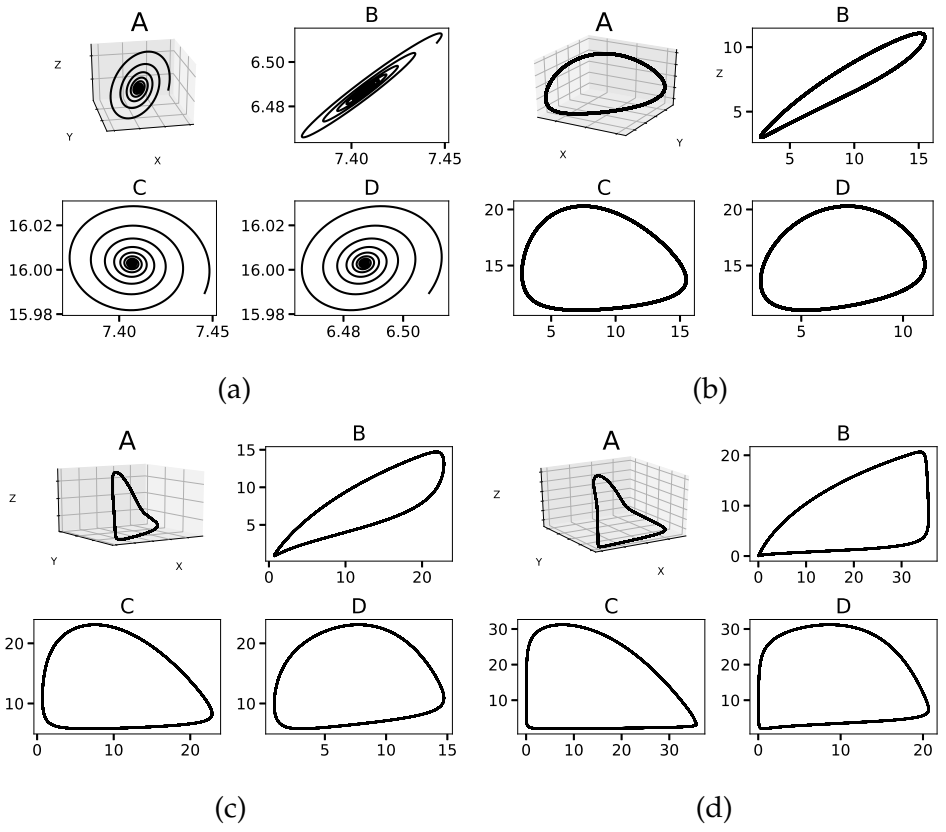


Figure 4.3: Phase portraits according to the change in the carrying capacity. In (a), $K_{12} = [22, 13]$; in (b), $K_{12} = [25, 15]$; in (c), $k_{12} = [28, 17]$ and in (d), $k_{ij} = [38, 22]$; where $K_{12} = [K_1, K_2]$. In all the figures, $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $h_0 = 1.25$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$.

From figure 4.3, we remark that the enrichment of the environment leads to larger fluctuations or amplitudes which can be seen by the increase in the size of (elongated) the phase portrait in the 3D space. The parameters' values with respect to figure 4.3 give respectively $(\lambda_1 \simeq -1.41, \lambda_2 \simeq -0.022 - 0.337i, \lambda_3 \simeq -0.022 + 0.337i)$; $(\lambda_1 \simeq -1.134, \lambda_2 \simeq 0.005 - 0.31i, \lambda_3 \simeq 0.005 + 0.31i)$; $(\lambda_1 \simeq -0.837, \lambda_2 \simeq -0.001 - 0.258i, \lambda_3 \simeq -0.001 + 0.258i)$ and $(\lambda_1 \simeq -0.71, \lambda_2 \simeq -0.006 - 0.201i, \lambda_3 \simeq -0.006 + 0.201i)$ as eigenvalues. And the associated equilibria are respectively $V \simeq (7.407, 6.487, 16.003)$; $V \simeq (9.105, 7.038, 15.657)$; $V \simeq (11.79, 7.792, 14.45)$ and $V \simeq (17.839, 10.351, 16.596)$. Thus, the

enrichment of the environment can both lead to stability and instability. In fact, in figures 4.3a, 4.3c and 4.3d we have an attracting focus while in figure 4.3b the equilibrium is a repelling saddle focus. Besides, an increase in the carrying capacity increases the size of the different prey population at equilibrium, but the predator population can either increase or decrease. The general effect of enriching the environment to our model can be resumed according to the bifurcation diagram 4.4.

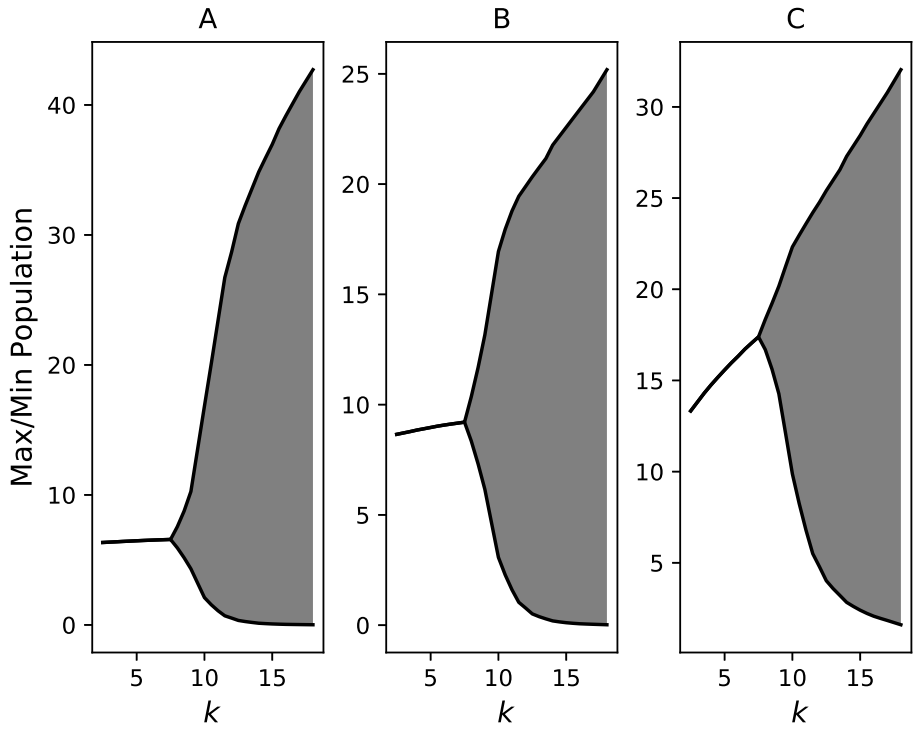
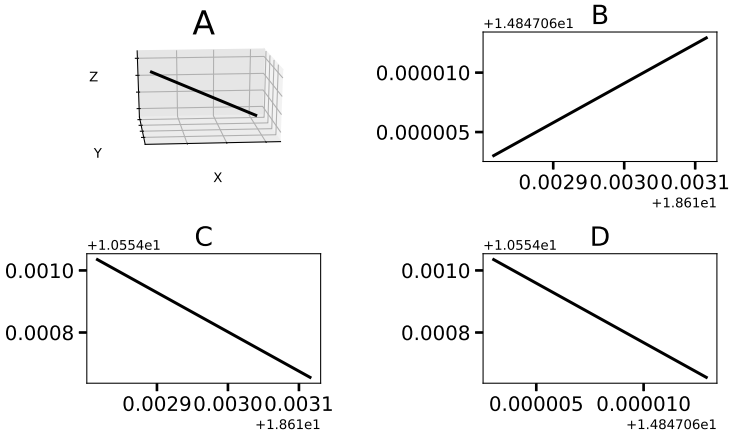
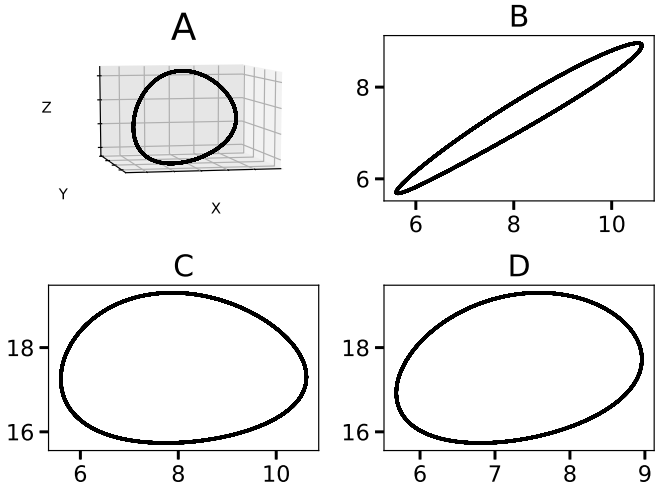


Figure 4.4: Bifurcation diagram with respect to the carrying capacity. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $h_0 = 1.25$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$.

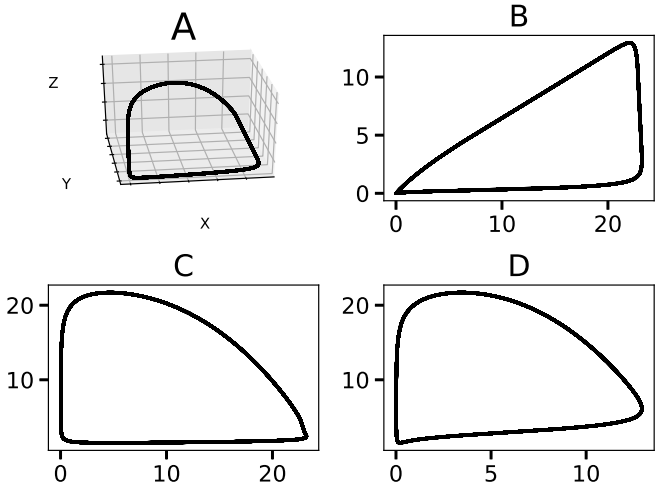
3. Effects of the allometry exponent



(a)



(b)



(c)

Figure 4.5: Phase portrait according to the change of the allometry exponent q. In (a), $q = -5.0$; in (b), $q = -1.25$ and in (c), $q = 0.0$. The other parameters are: $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $K_{12} = [25, 15]$, $h_0 = 1.25$, $m = 0.335$, $\mu = 0.55, \ell = 1$.

The dynamic of system 3.5 is affected by the allometry exponent q. In fact, varying q changes the success probability γ_i of the different prey. Logically increasing or decreasing q can either increase, decrease all the γ_i or increase some, and decrease some of the γ_i. Considering the set of parameter values in figure 4.5, changing q from -5 to respectively -1.25 and 0 increases the success rate of both prey types. This increase/decrease behaviour of the success rate is much more considerable for the prey having the highest relative body mass difference compared to the body mass for which the success probability is at its relative maximum. That is given for instance, two different prey types i and j, then γ_j will increase faster than γ_i if $\frac{|b_i - b_{max}|}{b_{max}} < \frac{|b_j - b_{max}|}{b_{max}}$; where b_{max} represents the body mass for which $\gamma(b_{max}) = 1$. Besides, varying q changes also the handling time H_i of the different prey types, since H_i depends on γ_i. An increase (respectively, decrease) of γ_i increases (respectively, decreases) the handling time H_i in our model formulation. This can be easily seen by checking the sign of the partial derivative of H_i with respect to γ_i.

The parameters' values with respect to figure 4.5 give respectively $(\lambda_1 \simeq -1.39, \lambda_2 \simeq -0.915, \lambda_3 \simeq -0.054)$; $(\lambda_1 \simeq -1.363, \lambda_2 \simeq 0.001 - 0.332i, \lambda_3 \simeq 0.001 + 0.332i)$ and $(\lambda_1 \simeq -1.062, \lambda_2 \simeq 0.032 - 0.256i, \lambda_3 \simeq 0.032 + 0.256i)$ as eigenvalues. And the associated equilibria are respectively $V \simeq (18.613, 14.847, 10.555)$;

$V \simeq (8.109, 7.321, 17.518)$ and $V \simeq (11.609, 6.470, 11.618)$. Thus, the change in the allometry exponent can lead to stability and instability. In fact, in figures 4.5b, and 4.5c we have a repelling saddle focus, while in figure 4.5a we have an attracting node. General overview of system (3.5) with respect to the change of the allometry exponent q can be resumed by the bifurcation diagram 4.6.

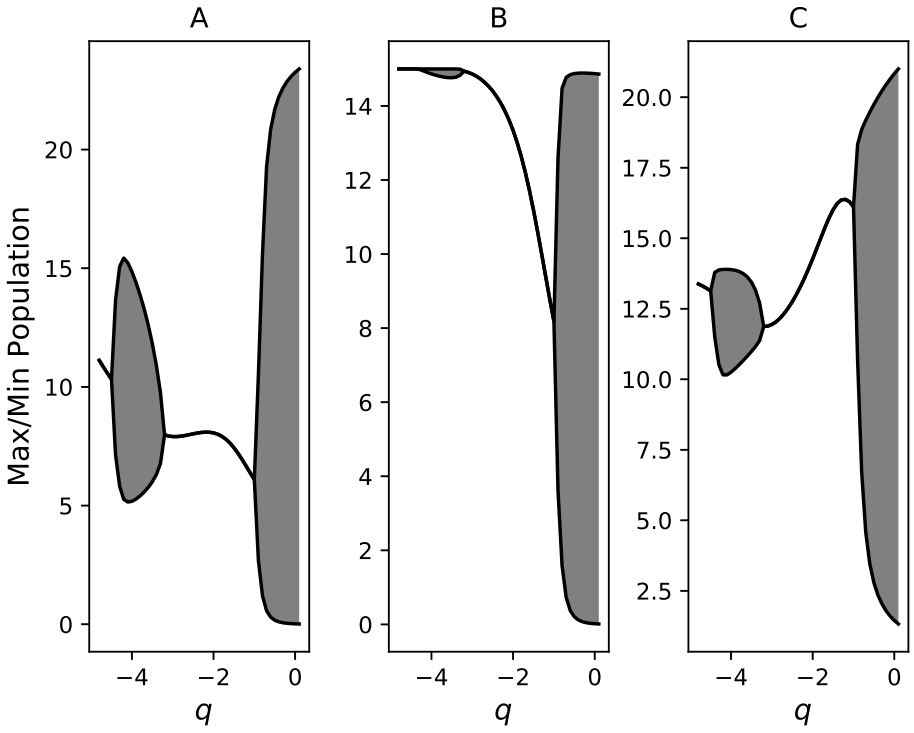
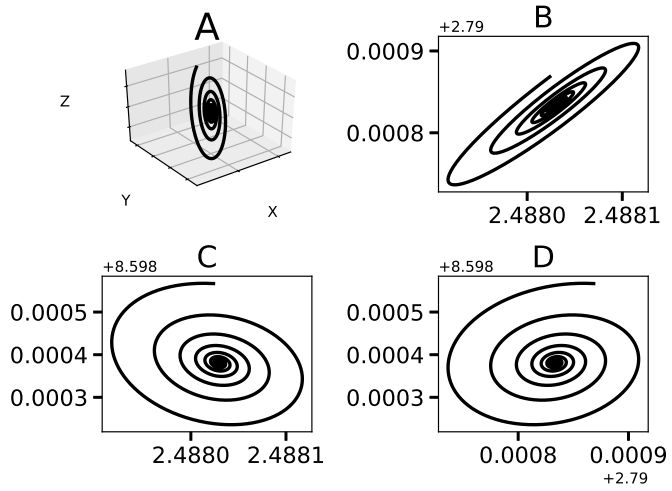
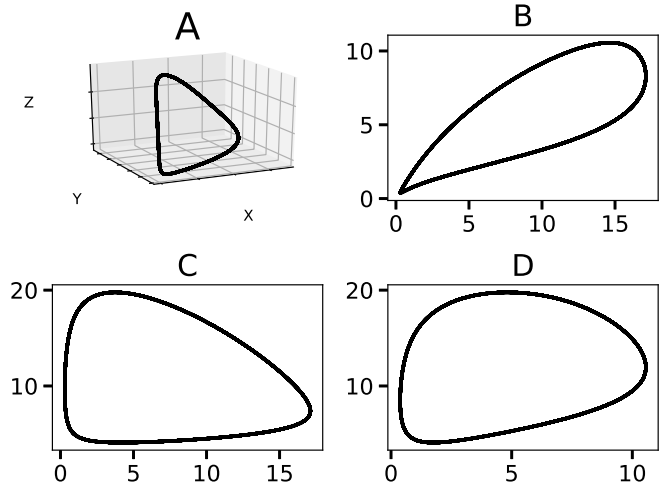


Figure 4.6: Bifurcation diagram with respect to the allometry exponent. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $h_0 = 1.25$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$, $K_{12} = [25, 15]$.

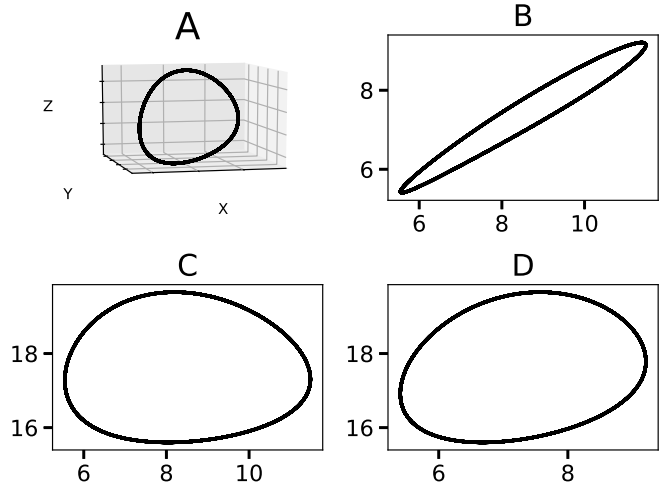
4. Effects of the handling time



(a)



(b)



(c)

Figure 4.7: Phase portrait according to the change of the handling time coefficient h_0. In (a) : $h_0 = 0.22$; (b) : $h_0 = 0.8$, (c) : $h_0 = 1.3$. The other parameters are kept constant $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $K_{12} = [25, 15]$, $q = -1.15$, $m = 0.335$, $\mu = 0.55, \ell = 1$.

The different parameters' values with respect to figure 4.7 give the following sets $(\lambda_1 \simeq -1.492, \lambda_2 \simeq -0.047 - 0.615i, \lambda_3 \simeq -0.047 + 0.615i)$; $(\lambda_1 \simeq -0.973, \lambda_2 \simeq 0.024 - 0.415i, \lambda_3 \simeq 0.024 + 0.415i)$ and $(\lambda_1 \simeq -1.343, \lambda_2 \simeq 0.001 - 0.319i, \lambda_3 \simeq 0.001 + 0.319i)$ as eigenvalues associated respectively to the following approximated equilibria
$(2.475, 2.627, 8.403)$; $(8.7, 5.470, 11.931)$ and $(8.513, 7.307, 17.626)$. Thus, varying the handling time for the different prey types can lead both to different kind of interior points. In figures 4.7b and 4.7c, we have a repelling saddle focus; figure 4.7a represents an attracting focus. Besides, we note that an increase in the handling time increases species' population density at equilibrium. However, when the handling time for the different prey gets relatively large, predator population might be driven to extinction (see figure 4.8).

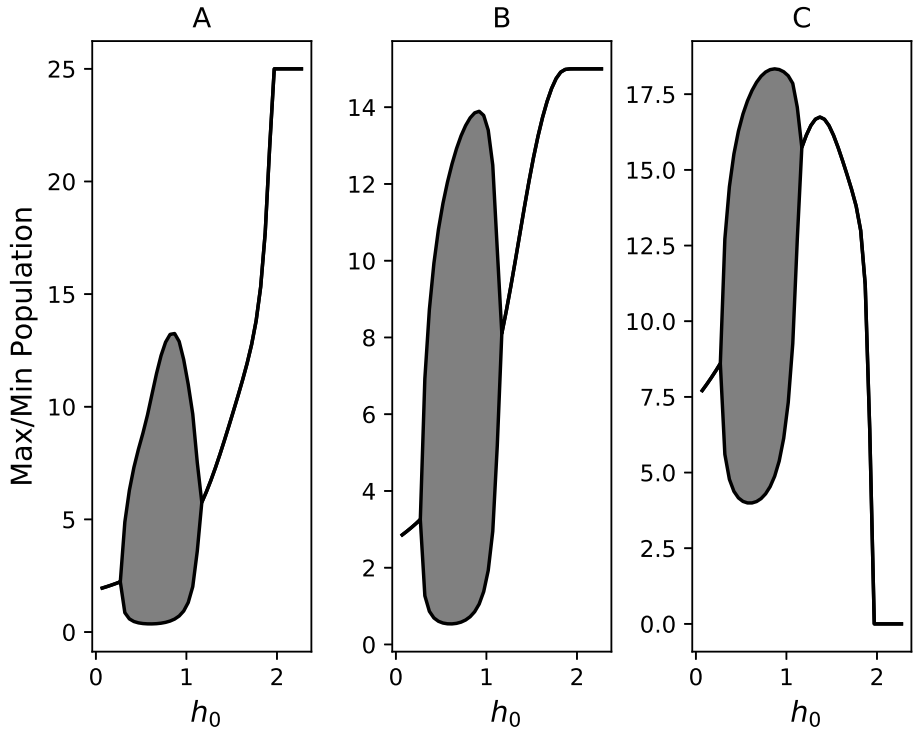
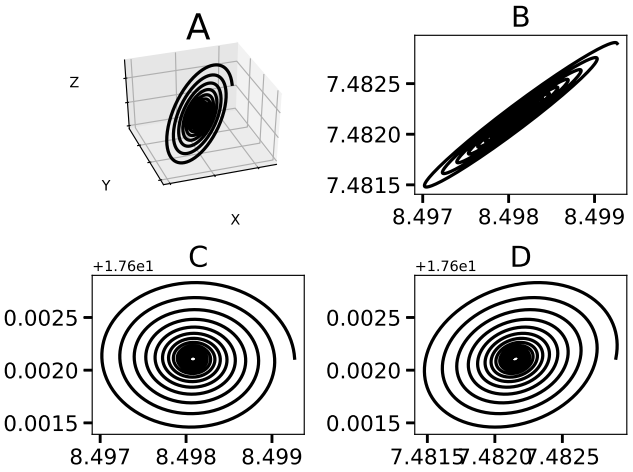
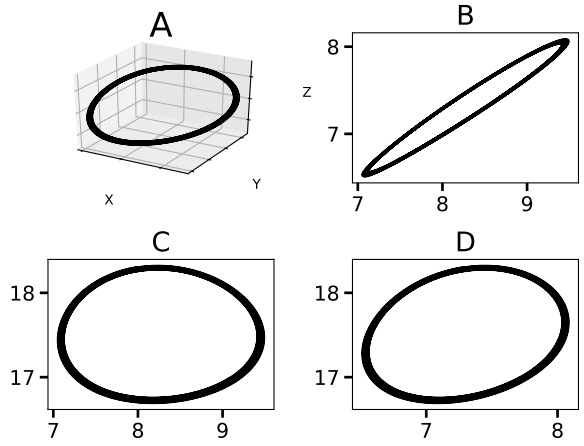


Figure 4.8: Bifurcation diagram with respect to the handling time. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$, $K_{12} = [25, 15]$.

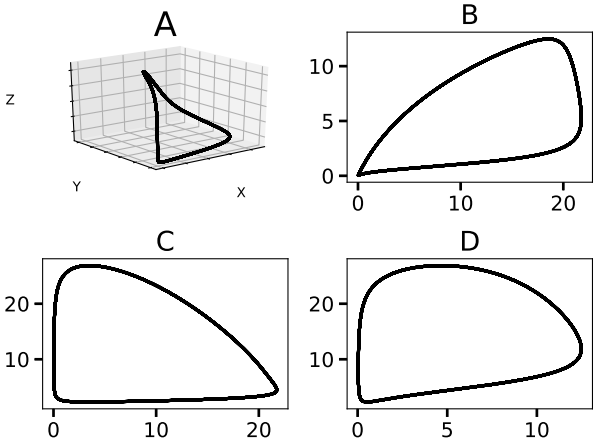
4.2.2 Effects of Predator Components



(a)



(b)



(c)

Figure 4.9: Phase portrait according to the change of the conversion efficiency coefficient c_0. In (a) : $c_0 = 0.72$; (b) : $c_0 = 0.7275$; (c) : $c_0 = 0.975$. The parameters are kept constant; $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $K_{12} = [25, 15]$, $h_0 = 1.25$, $q = -1.15$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$.

From figure 4.9, we remark that system (3.5) is affected by the change in the predator conversion efficiency. The different parameters' values give the following ($\lambda_1 \simeq -1.405$, $\lambda_2 \simeq -0.113 - 0.323i$, $\lambda_3 \simeq -0.113 + 0.323i$); ($\lambda_1 \simeq -1.4$, $\lambda_2 \simeq -0.327$, $\lambda_3 \simeq 0.327i$) and ($\lambda_1 \simeq -0.832$, $\lambda_2 \simeq 0.026 - 0.293i$, $\lambda_3 \simeq 0.026 + 0.293i$) as eigenvalues associated respectively to the following approximated equilibria (8.5, 7.482, 17.602); (8.269 7.299, 17.513) and (10.890, 6.257, 14.590).

Thus, varying the predator's conversion efficiency can lead both in attracting and repelling interiors. In figure 4.9a, we have an attracting focus since all the real part of the eigenvalues corresponding to $c_0 = 0.72$ are strictly negative real numbers; figure 4.9b represents an attractive centre and figure 4.9c a repelling saddle node. Besides, a relatively small conversion efficiency factor might drive the predator population to extinction and an increase in this factor might increase or decrease the predator population at equilibrium while decreasing or increasing the population density of the different prey types. Thus, the behaviour of the system (3.5) according to the change of the conversion efficiency can be resumed by the figure 4.10.

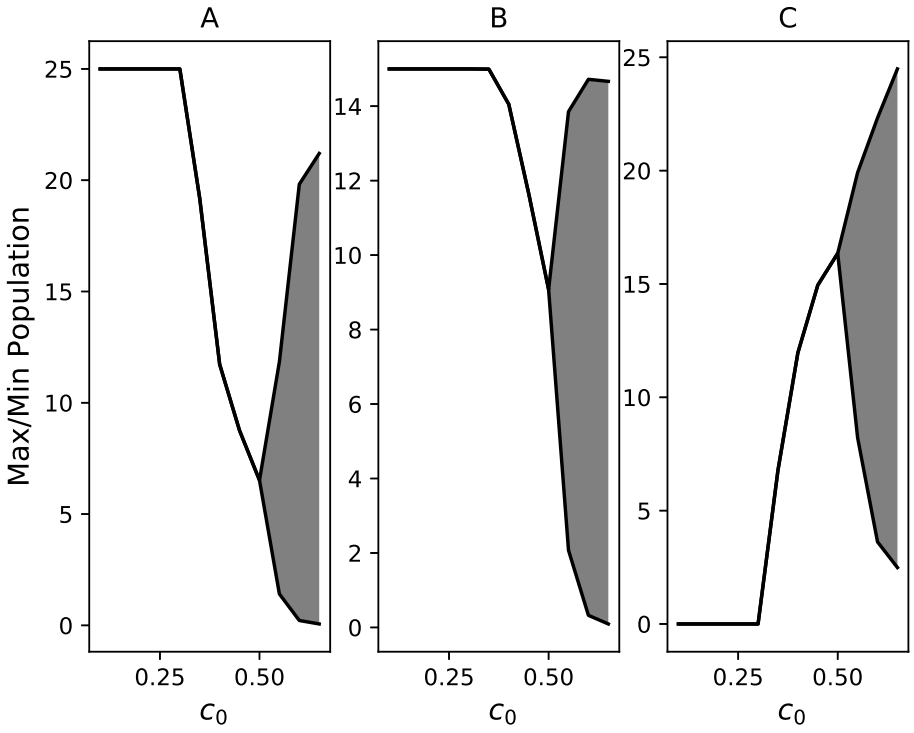


Figure 4.10: Bifurcation diagrams with respect to the predator's conversion efficiency. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $q = -1.15$, $h_0 = 1.25$, $m = 0.335$, $\mu = 0.55$, $\ell = 1$, $K_{12} = [25, 15]$.

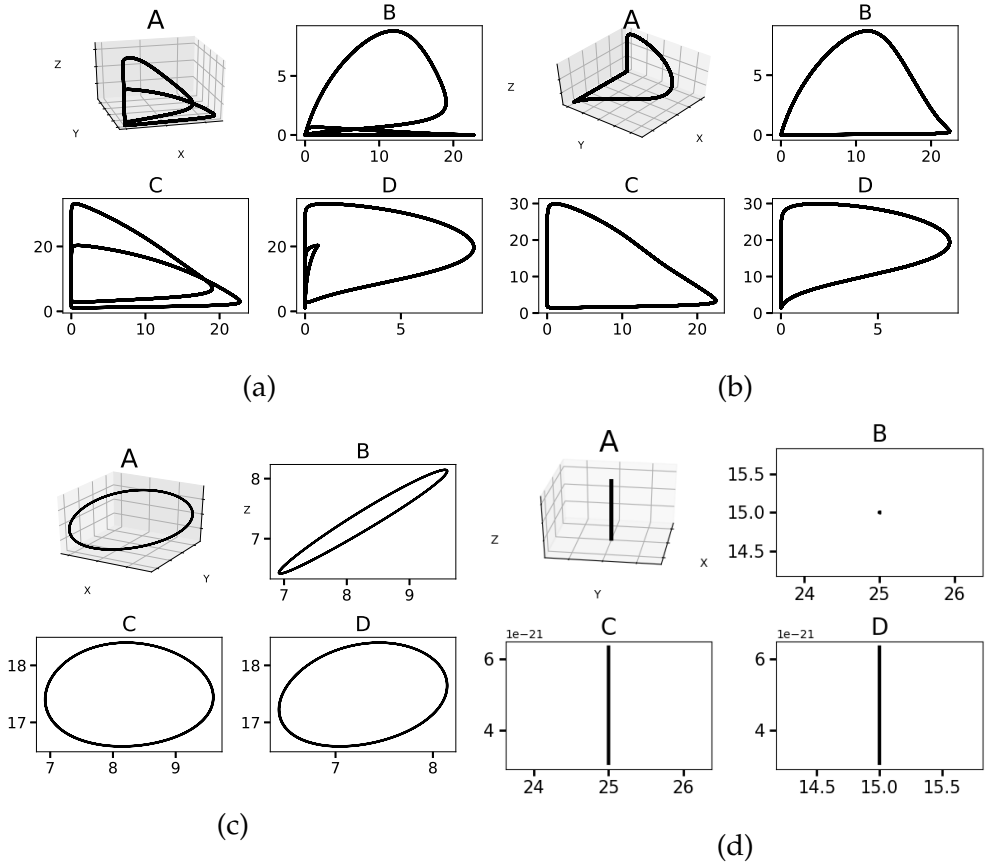


Figure 4.11: Phase portrait according to the change of the predator mortality rate m. In (a), $m = 0.1$; in (b), $m = 0.15$; in (c), $m = 0.345$ and in (d), $m = 0.65$. The other parameters are, $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c = 0.75$, $K_{12} = [25, 15]$, $q = -1.15$, $h_0 = 1.25$, $\mu = 0.55$, $\ell = 1$.

We remark from figure 4.11, that varying the predator's mortality rate m affects system (3.5) dynamics. Considering the set of parameter values from figure 4.11, we have

(a):

- A repelling saddle focus

$$(11.382,\ 4.403,\ 17.127);$$

$$(\lambda_1 \simeq -0.704,\ \lambda_2 \simeq 0.128 - 0.203i,\ \lambda_3 \simeq 0.128 - 0.203i);$$

- A repelling focus

$$(9.514,\ 0.338,\ 11.572);$$

$$(\lambda_1 \simeq 0.841,\ \lambda_2 \simeq 0.196 - 0.432i,\ \lambda_3 \simeq 0.196 + 0.432i)$$

(b): • A repelling saddle focus

$$(11.237,\ 4.349,\ 15.680)$$

$$(\lambda_1 \simeq -0.573,\ \lambda_2 \simeq 0.103 - 0.19i,\ \lambda_3 \simeq 0.103 + 0.19i).$$

(c): • An attracting center

$$(8.259,\ 7.283,\ 17.489$$

$$(\lambda_1 \simeq -1.393,\ \lambda_2 \simeq -0.331i,\ \lambda_3 \simeq 0.332i).$$

(d): • An attracting node

$$(25,\ 15,\ 0);$$

$$(\lambda_1 \simeq -2.42,\ \lambda_2 \simeq -0.92,\ \lambda_3 \simeq -0.199).$$

Thus, varying m can lead to stability (sub-figure 4.11c) or instability (sub-figures 4.11a and 4.11b) of system (3.5). Besides, a significant per capita death rate could eventually lead the predator population to extinction (as we can see from figure 4.11d). In sub-figure 4.11a the system oscillates successively around two main points, this might indicate a period doubling (with a decrease of the mortality rate) or period halving (with an increase of the mortality rate). We will explore more on these situations in the next section using wavelet analysis on the time series of system 3.5. Figure 4.12 gives a general view of the effect of the mortality rate of the predators of the system (3.5) dynamics.

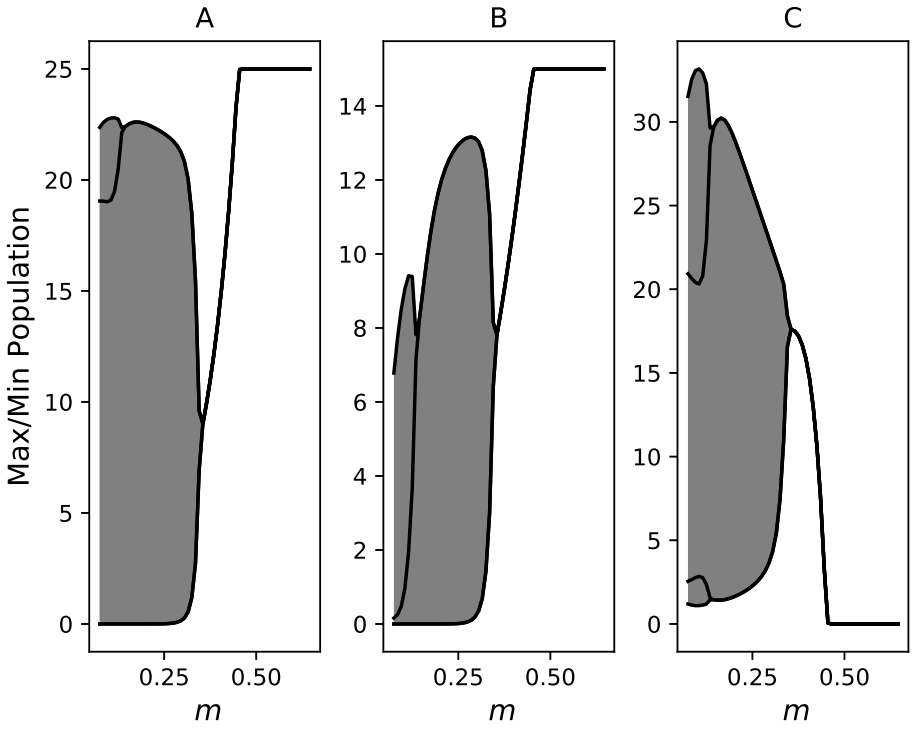


Figure 4.12: Bifurcation diagrams with respect to the predator's per capita mortality rate. $b_1 = 0.6$, $b_2 = 1.2$, $b = 1.5$, $c_0 = 0.75$, $h_0 = 1.25$, $q = -1.15$, $\mu = 0.55$, $\ell = 1$, $K_{12} = [25, 15]$.

4.2.3 Wavelet analysis

Wavelets are practical tool for analysing localised variations of power within a time series (signal) [35, 15, 7]. Unlike some methods such as Fourier transforms, that provide information (non localised in time) on spectral components of a time series and assume stationarity of signals, wavelet transforms decompose time series into time-frequency domain. Thus, allowing to find localised spectral contents of a signal. Besides, wavelet transforms are free of the stationarity assumption and therefore are more suitable for real-life time series analysis.

For our analysis, the Morlet wavelet basis function is used, and the transform is performed using the method described in [35]. Numerical simulations on this section is done using the Python wavelet software provided by Evgeniya Predybaylo based on [34]. To reduce wraparound effects, we padded our time series with zeros. Figures 4.13, 4.14 and 4.15 show the time

series of the predator population and describe the dominant modes of variability of the time series according to the change in the predator mortality rate.

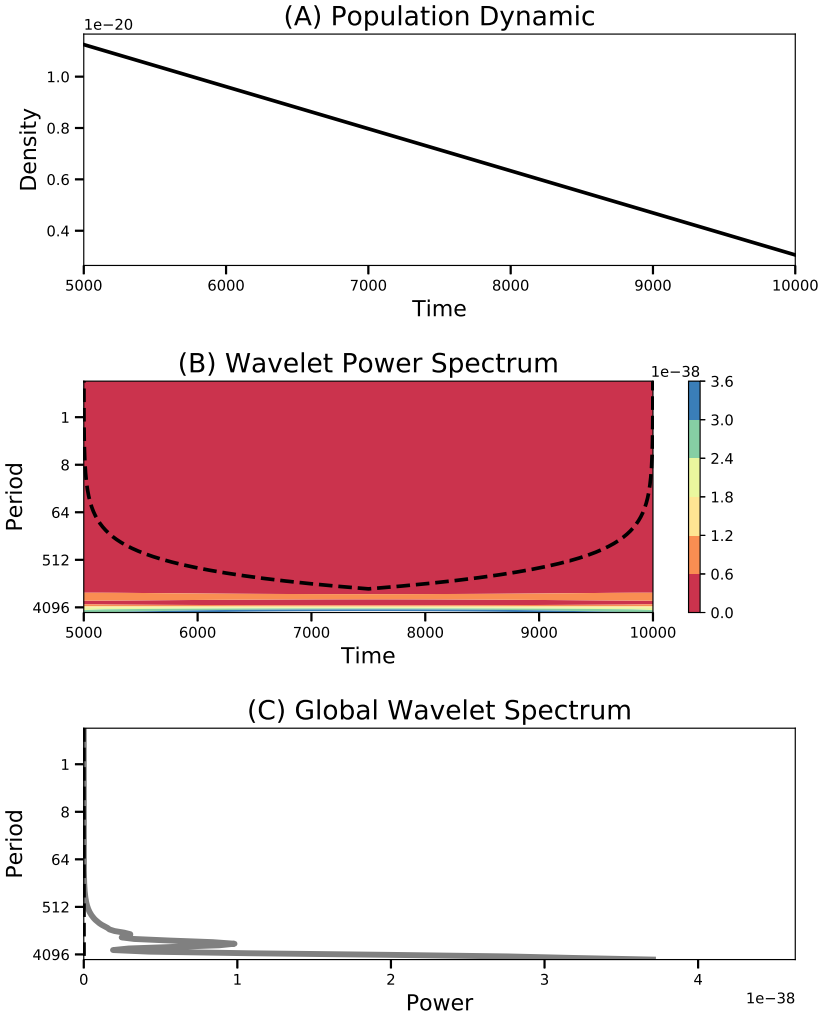


Figure 4.13: (A) Predator population dynamic at $m = 0.65$; (B) The Morlet wavelet power spectrum of the time series in (A). Region under the dashed line represents the "cone-of-influence,"where zero padding is used.

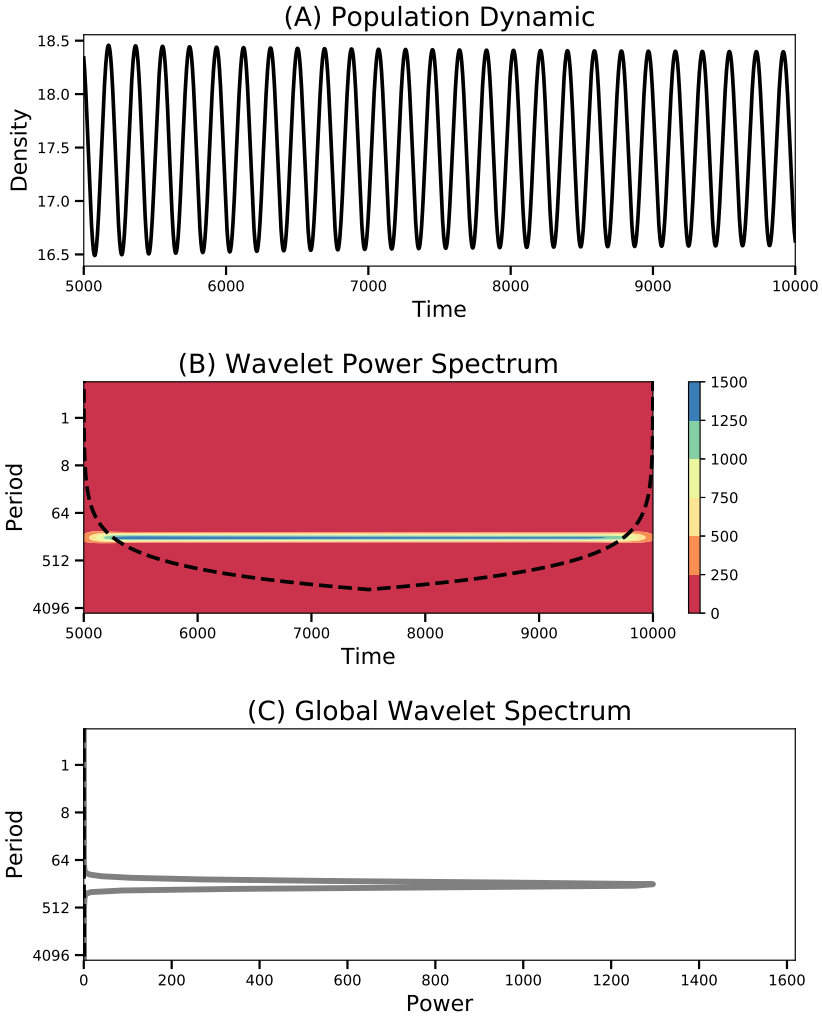


Figure 4.14: (A) Predator population dynamic at $m = 0.345$; (B) The Morlet wavelet power spectrum of the time series in (A). Region under the dashed line represents the "cone-of-influence,"where zero padding is used.

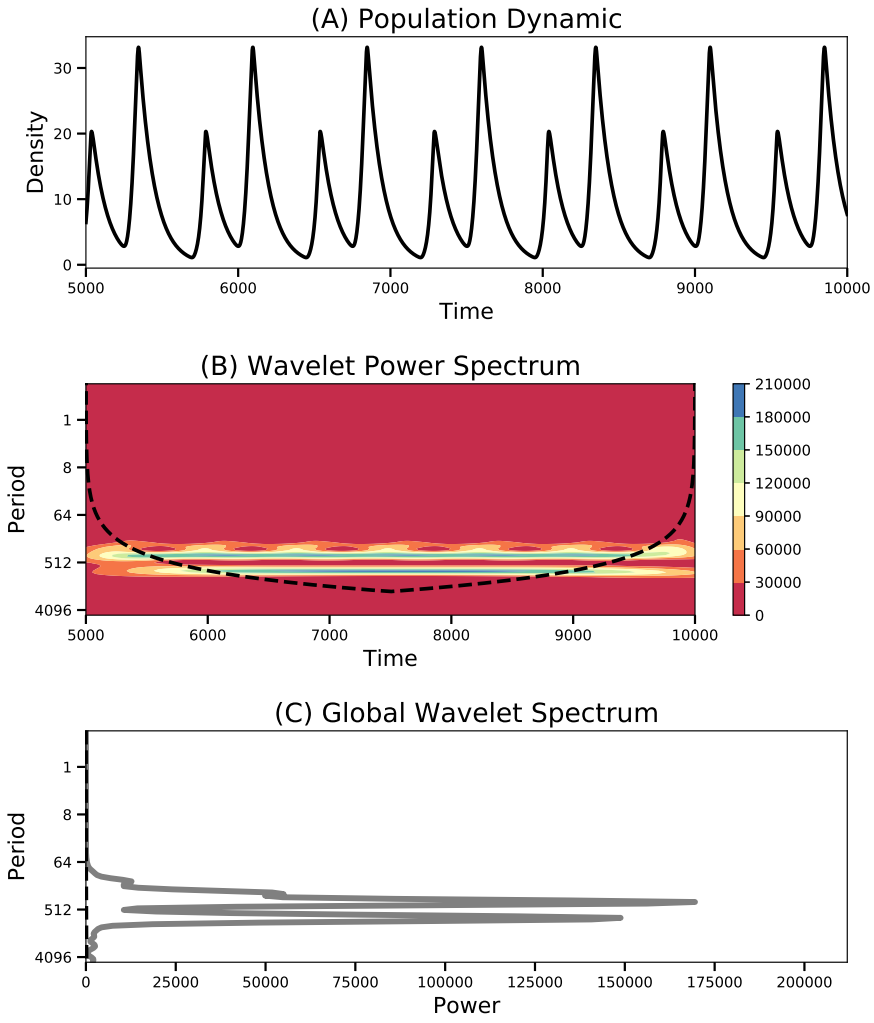


Figure 4.15: (A) Predator population dynamic at $m = 0.1$; (B) The Morlet wavelet power spectrum of the time series in (A). Region under the dashed line represents the "cone-of-influence,"where zero padding is used.

When $m = 0.65$, we remark from figure 4.13 that the predator population is driven to extinction and that there is no cyclic component which can be seen from the wavelet power spectrum figure and the global wavelet spectrum. When m decreases to 0.345, we note the presence of limit cycles (4.14 (A)) and the wavelet power spectrum shows the period of oscillation (with a strong power) of the predator population and the oscillation occurs over the whole time interval. At $m = 0.1$, we observe oscillations around mainly two points from the predator population dynamic (refer figure 4.15 (A)) and the wavelet power spectrum and the global wavelet spectrum show the pres-

ence of two strong periodic components with 95% over the whole time interval. Besides, we remark the presence of some transients (figure 4.15 (B) and (C)) which are not observable from the population dynamics figure. These transients can lead to chaos. The same behaviour observed with the predator population while varying the predator's mortality rate is observed also within the two different prey populations.

4.3 Random foraging or Adaptive (Optimal) Foraging ?

Theorem 2. Random foraging ($\ell = 0$) is not always the worst and intermediate values of the switching exponent ℓ can benefit less to the predator (i.e, intermediate level of adaptiveness can be costly compared to random foraging).

Proof. Using Taylor's expansion of α_i with two prey types, let us derive the predator equilibrium. The function $\alpha_i(\ell) = \dfrac{(e_i V_i)^\ell}{\sum_{j=1}^{n} (e_j V_j)^\ell}$ is infinitely differentiable at zero and therefore can be written as a power series (Taylor series) as:

$$\alpha_i(l) = \alpha_i(0) + \frac{\ell}{1!}\frac{d\alpha_i(0)}{d\ell} + \frac{\ell^2}{2!}\frac{d^2\alpha_i(0)}{d\ell^2} + \frac{\ell^3}{3!}\frac{d^3\alpha_i(0)}{d\ell^3} + \cdots$$

Considering only the first degree polynomial of the power series of the attack probability and two prey types, we have:

$$\alpha_i(\ell) = \frac{1}{2} + \ell \left[\frac{(e_i V_i)^\ell \left(\ln(e_i V_i) \left((e_1 V_1)^\ell + (e_2 V_2)^\ell \right) - (e_1 V_1)^\ell \ln(e_1 V_1) - (e_2 V_2)^\ell \ln(e_2 V_2) \right)}{\left(\sum_{j=1}^{2} (e_j V_j)^\ell \right)^2} \right]_{\ell=0} + \mathcal{O}(\ell^2)$$

$$\Rightarrow \alpha_i(\ell) = \frac{1}{2} + \ell \left[\frac{2\ln(e_i V_i) - \ln(e_1 V_1) - \ln(e_2 V_2)}{4} \right] + \mathcal{O}(\ell^2)$$

and thus, we have the following attack probabilities:

$$\alpha_1(\ell) = \frac{1}{2} + \frac{\ell}{4} \ln\left(\frac{e_1 V_1}{e_2 V_2} \right);$$

$$\alpha_2(\ell) = \frac{1}{2} - \frac{\ell}{4} \ln\left(\frac{e_1 V_1}{e_2 V_2} \right).$$

System 3.5 in that case can be rewritten as:

$$\begin{cases} \dot{V}_1 &= r_1 V_1 \left(1 - \dfrac{V_1}{K_1}\right) - \dfrac{\left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) \gamma_1 V_1}{4 + \left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_2 V_2} P \\ \dot{V}_2 &= r_2 V_2 \left(1 - \dfrac{V_2}{K_2}\right) - \dfrac{\left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) \gamma_2 V_2}{4 + \left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_2 V_2} P \\ \dot{P} &= P \dfrac{\left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) c_1 \gamma_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) c_2 \gamma_2 V_2}{4 + \left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_2 V_2} - mP. \end{cases} \tag{4.6}$$

Note that when there is only one prey type, then the equilibria do not depend on the switching exponent since $\alpha_i = 1$ and therefore are equivalent to $(V_1^{13}, 0, P^{13})$ and $(0, V_2^{23}, P^{23})$. Considering that all the three species coexist, the equilibrium is given by:

$$P^* = \frac{r_1(K_1 - V_1^*)\left[4 + \left(2 + \ell \ln\left(\frac{e_1 V_1^*}{e_2 V_2^*}\right)\right) H_1 V_1^* + \left(2 - \ell \ln\left(\frac{e_1 V_1^*}{e_2 V_2^*}\right)\right) H_2 V_2^*\right]}{\gamma_1 K_1 \left(2 + \ell \ln\left(\frac{e_1 V_1^*}{e_2 V_2^*}\right)\right)};$$

V_1^* and V_2^*; where V_1^*, V_2^* are solution of the following system:

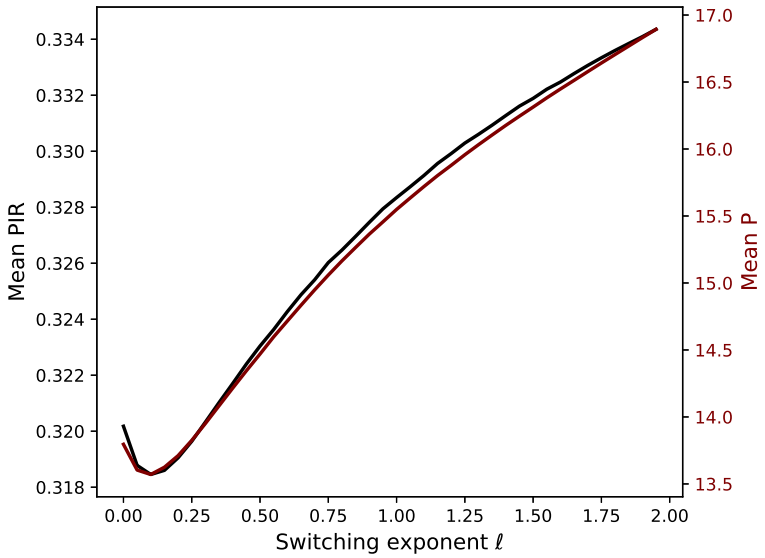
$$\begin{cases} 2(a_1 K_2 - a_2 K_1) + a_2 V_1 \left[2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right] - a_1 V_2 \left[2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right] + \\ \qquad + \ell (a_1 K_2 + a_2 K_1) \ln\left(\dfrac{e_1 V_1}{e_2 V_2}\right) = 0 \\ \dfrac{\left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) d_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) d_2 V_2}{4 + \left(2 + \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_1 V_1 + \left(2 - \ell \ln\left(\frac{e_1 V_1}{e_2 V_2}\right)\right) H_2 V_2} - m = 0; \end{cases} \tag{4.7}$$

where $a_1 = r_2 \gamma_1 K_1$; $a_2 = r_1 \gamma_2 K_2$ and $d_i = c_i \gamma_i$. Note that P^* exists if $2 > -\ell \ln\left(\dfrac{e_1 V_1^*}{e_2 V_2^*}\right)$. The derivative of P^* with respect to ℓ is given by

$$\frac{\partial P^*}{\partial \ell} = \frac{-4 r_1 \gamma_1 K_1 (K_1 - V_1^*)(1 + H_2 V_2^*) \ln\left(\dfrac{e_1 V_1^*}{e_2 V_2^*}\right)}{\left[\gamma_1 K_1 \left(2 + \ell \ln\left(\dfrac{e_1 V_1^*}{e_2 V_2^*}\right)\right)\right]^2}.$$

Since at equilibrium (with all species coexisting) prey population are always strictly less than their carrying capacity, it is easily seen that when the total benefit of the more profitable $e_1 V_1^*$ is greater than the total benefit of the alternate prey type $e_2 V_2^*$, $\frac{\partial P^*}{\partial \ell} < 0$ and therefore random foraging performs better than adaptive foraging while when the total benefit of the most profitable prey is less than the total benefit of the alternative prey, adaptive foraging performs better than random foraging $\frac{\partial P^*}{\partial \ell} > 0$.
Figure 4.16b illustrates the case when random foraging is worth considering with respect to significant level of adaptiveness. This can be due to a non rich environment (low carrying capacity). While the environment is relatively rich, figure 4.16a shows an example where random foraging performs better than being slightly adaptive but less benefit than optimal foraging.

(a)



(b)

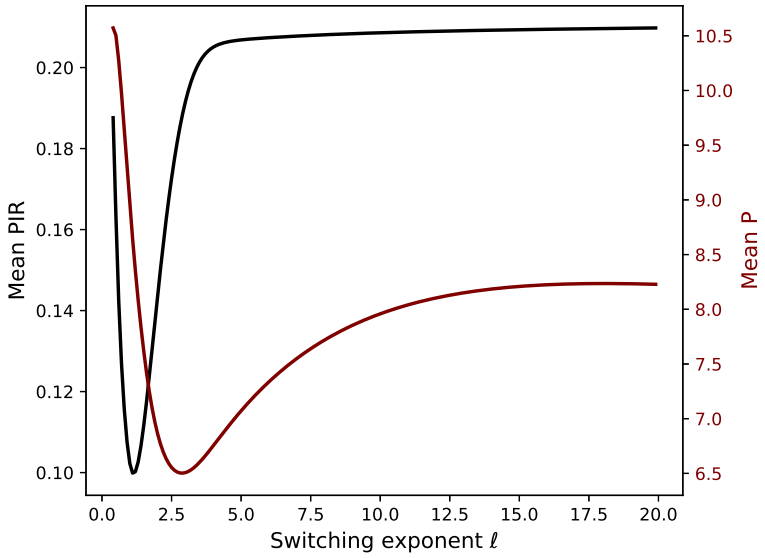


Figure 4.16: Mean of per-capita intake rate and predator population according to predator adaptiveness level measured by the switching exponent l. In (a), simulation is done with two prey types while in (b) the system consists of five different prey types.

4.4 Discussion

In this chapter, we discussed the dynamics of our model analytically and numerically considering two different prey population types and a predator population. More precisely, we studied the effects of the switching exponent, the enrichment of the environment, the conversion efficiency, the allometry exponent, the handling time and the predator mortality rate on the population dynamics of our model. In addition, numerical simulations with five distinct prey types were carried out in the analysis of the predator population density and predator per capita intake rate dynamics. The case when the adaptiveness level is equal to zero is described as random foraging and the predator can be qualified as a non-adaptive generalist or random forager and has been studied analytically. When in addition of being a random forager, the predator searches for the different prey at the same rate, and when the different prey types have the same growth rate and efficiency of success, local stability may occur at the all species equilibrium for some values of the predator mortality rate strictly inside an interval defined by the different system parameters. However, system (3.5) displays larger permanence region with an increasing in the adaptiveness coefficient. This is due to the fact that increasing ℓ can lead to either stability or partial stability (decreasing in the amplitude of oscillations). Thus, adaptive foraging leads to greater permanence region than random foraging. A similar result has been found in [25], where it has been proven with a classical optimal diet model that optimal foraging performs better than random foraging in term of preserving the permanence of a predator-prey system. In our model, optimal foraging (zero-one rule) can be observed for large values of the adaptiveness level.

For values of ℓ such that $\ell > 0$, analytical study of the coexistence of all species equilibrium is very complex. However, when ℓ is close to zero, we suggest from **Theorem 2** that when the total benefit of the most profitable prey is greater than the total benefit of the alternate prey, intermediate adaptiveness benefits less to the predator population. Therefore, random foraging may in certain cases be worth considering for foragers that consider intermediate values of the exponent ℓ. Besides, random foraging will be worth considering when the environment is poor in term of resources (that

is when prey types have low carrying capacity) with respect to optimal foraging. This result formalises the intuitive idea of "taking any resource encountered when resources are scarce".

Chapter 5

Conclusion and Perspectives

The need for more plausibility in the description of predator-prey interactions have led to the inclusion of some physiological constraints into the formulation of predator's response. Such inclusion resulted principally into the paradigm of optimal diet models, and predator-prey switching models. However, recent literature on consumer-resource dynamics has discussed separately those two concepts, though real systems may generally be a compromise of the two. Besides, these improved realisms into the formulation of functional responses resulted in very complex mathematical expressions which render their dynamics almost inaccessible.

In this project, we formulated and analysed a generalised predator-prey model (AODM) under different level of consumer's adaptiveness and thus allowing for both predator switching and maximization of food intake. Particularly, the formulation of our AODM includes a mechanistic derivation of a generalised type 2 response that accounts in addition for time wasted for unsuccessful attacks by a predator. Besides, we assume some of the predator and prey components to be function of body mass since most of species traits or functions can be derived from their metabolic rate and allometry scaling. However, note that this latter assumption does not affect the results of our analysis, but instead serves as a base to formulate certain component of the AODM as the efficiency of a successful attack. Boundedness, existence and uniqueness of solutions of our model are proved and the switching criterion is verified.

One of the results of this project suggests that adaptiveness in predator-

prey systems promotes (partial) stability and thus may be a substantial factor to maintaining biodiversity within communities. Most importantly, we demonstrated that zero-adaptiveness (random foraging) is not always the worst scenario as regarded by optimal foraging theory. But instead, may be worth considering, especially for consumers associated with intermediate levels of adaptiveness. The AODM model can be used, for example, to understand how the changes in the characteristics of prey and predator (carrying capacity, level of adaptiveness, handling time, conversion efficiency, predator mortality rate, allometry exponent) affect the predator intake and what could be the specialization level or the best strategy to adopt in changing environments.

Note also that the formulation of our model is not without limitations. Throughout this work, we assumed a closed environment, one type of predator, constant mortality rate, and the absence of competition among and within the different prey types. This is rarely the case of natural environments. In addition, the predator-prey body size relation may depend on the nature of the environment (terrestrial or aquatic). Thus, incorporating these factors might be an important step in accessing the generality of the aforementioned results.

List of References

[1] P. A. Abrams. The effects of adaptive behavior on the type-2 functional response. *Ecology*, 71(3):877–885, 1990.

[2] A. A. Aljetlawi, E. Sparrevik, and K. Leonardsson. Prey–predator size-dependent functional response: derivation and rescaling to the real world. *Journal of Animal Ecology*, 73(2):239–252, 2004.

[3] K. J. Anderson-Teixeira, V. M. Savage, A. P. Allen, and J. F. Gillooly. Allometry and metabolic scaling in ecology. *eLS*, 2009.

[4] V. Baudrot, A. Perasso, C. Fritsch, P. Giraudoux, and F. Raoul. The adaptation of generalist predators' diet in a multi-prey context: insights from new functional responses. *Ecology*, 97(7):1832–1841, 2016.

[5] S. Bengtson. Origins and early evolution of predation. *Paleontological Society Papers*, 8:289–318, 2002.

[6] A. A. Berryman. The orgins and evolution of predator-prey theory. *Ecology*, 73(5):1530–1535, 1992.

[7] B. Cazelles, M. Chavez, D. Berteaux, F. Ménard, J. O. Vik, S. Jenouvrier, and N. C. Stenseth. Wavelet analysis of ecological time series. *Oecologia*, 156(2):287–304, 2008.

[8] E. Charnov and G. H. Orians. Optimal foraging: some theoretical explorations. 2006.

[9] J. Chattopadhyay, N. Pal, S. Samanta, E. Venturino, and Q. Khan. Chaos control via feeding switching in an omnivory system. *Biosystems*, 138:18–24, 2015.

[10] R. Cressman, V. Křivan, J. S. Brown, and J. Garay. Game-theoretic methods for functional response and optimal foraging behavior. *PLoS One*, 9(2):e88773, 2014.

[11] J. P. DeLong, T. C. Hanley, and D. A. Vasseur. Predator–prey dynamics and the plasticity of predator body size. *Functional ecology*, 28(2):487–493, 2014.

[12] M. Denny. Buzz holling and the functional response. *The Bulletin of the Ecological Society of America*, 95(3):200–203, 2014.

[13] W. Gentleman, A. Leising, B. Frost, S. Strom, and J. Murray. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep Sea Research Part II: Topical Studies in Oceanography*, 50(22):2847–2875, 2003.

[14] N. J. Gotelli et al. *A primer of ecology.* Sinauer Associates Incorporated, 1995.

[15] A. Grinsted, J. C. Moore, and S. Jevrejeva. Application of the cross wavelet transform and wavelet coherence to geophysical time series. *Nonlinear processes in geophysics*, 11(5/6):561–566, 2004.

[16] P. Holgate et al. A prey-predator model with switching effect. *Journal of Theoretical Biology*, 125(1):61–66, 1987.

[17] C. S. Holling. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist*, 91(05):293–320, 1959.

[18] C. S. Holling. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(07):385–398, 1959.

[19] J. M. Jeschke, M. Kopp, and R. Tollrian. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, 72(1):95–112, 2002.

[20] G. Kalinkat, B. C. Rall, O. Vucic-Pestic, and U. Brose. The allometry of prey preferences. *PloS one*, 6(10):e25937, 2011.

[21] G. Kalinkat, F. D. Schneider, C. Digel, C. Guill, B. C. Rall, and U. Brose. Body masses, functional responses and predator–prey stability. *Ecology letters*, 16(9):1126–1134, 2013.

[22] M. Koen-Alonso. A process-oriented approach to the multispecies functional response. In *From energetics to ecosystems: the dynamics and structure of ecological systems*, pages 1–36. Springer, 2007.

[23] V. Křivan. Effects of optimal antipredator behavior of prey on predator–prey dynamics: the role of refuges. *Theoretical population biology*, 53(2):131–142, 1998.

[24] V. Křivan and J. Eisner. Optimal foraging and predator–prey dynamics iii. *Theoretical population biology*, 63(4):269–279, 2003.

[25] V. Křivan and A. Sikder. Optimal foraging and predator–prey dynamics, ii. *Theoretical Population Biology*, 55(2):111–126, 1999.

[26] W. W. Murdoch. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological monographs*, 39(4):335–354, 1969.

[27] A. Oaten and W. W. Murdoch. Switching, functional response, and stability in predator-prey systems. *The American Naturalist*, 109(967):299–318, 1975.

[28] B. C. Rall, G. Kalinkat, D. Ott, O. Vucic-Pestic, and U. Brose. Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, 120(4):483–492, 2011.

[29] V. M. Savage, J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. Effects of body size and temperature on population growth. *The American Naturalist*, 163(3):429–441, 2004.

[30] T. W. Schoener. A brief history of optimal foraging ecology. In *Foraging behavior*, pages 5–67. Springer, 1987.

[31] M. Solomon. The natural control of animal populations. *The Journal of Animal Ecology*, pages 1–35, 1949.

[32] D. W. Stephens and J. R. Krebs. *Foraging theory*. Princeton University Press, 1986.

[33] M. Tansky. Switching effect in prey-predator system. *Journal of Theoretical Biology*, 70(3):263–271, 1978.

[34] C. Torrence and G. Compo. Wavelet software. *See http://paos. colorado. edu/research/wavelets/software. html. b*, 1998.

[35] C. Torrence and G. P. Compo. A practical guide to wavelet analysis. *Bulletin of the American Meteorological society*, 79(1):61–78, 1998.

[36] S. M. Vallina, B. Ward, S. Dutkiewicz, and M. Follows. Maximal feeding with active prey-switching: A kill-the-winner functional response and its effect on global diversity and biogeography. *Progress in Oceanography*, 120:93–109, 2014.

[37] O. Vucic-Pestic, B. C. Rall, G. Kalinkat, and U. Brose. Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology*, 79(1):249–256, 2010.

[38] J. S. Weitz and S. A. Levin. Size and scaling of predator–prey dynamics. *Ecology letters*, 9(5):548–557, 2006.

[39] F. Zhang and C. Hui. Recent experience-driven behaviour optimizes foraging. *Animal behaviour*, 88:13–19, 2014.